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ALAIN LENOIR, GERARD ARNOLD & MICHEL LEPAGE (EDS)

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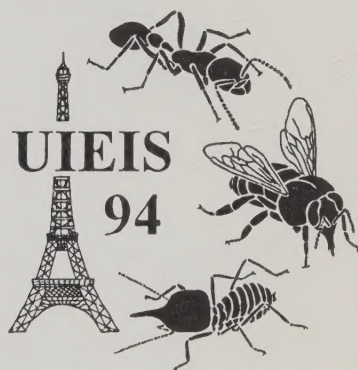
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PREFACE

Pierre Jaisson

Président de l'UIEIS / *President of IUSSI*

L'Union Internationale pour l'Etude des Insectes Sociaux (UIEIS) a été créée voici bientôt un demi-siècle par une poignée de chercheurs européens résolus, en particulier français et allemands. Aujourd'hui, l'Union compte un millier de membres et le congrès de Paris marquera une nouvelle étape de son développement puisqu'elle incorporera nombre de chercheurs de l'ex Union Soviétique et de la Chine.

Ce développement constant de l'UIEIS traduit non seulement l'intérêt des biologistes pour les sociétés d'insectes mais aussi l'impact de ces derniers sur les écosystèmes naturels ou modifiés par l'Homme.

Le contenu du XII^e Congrès de l'UIEIS, résumé dans cet ouvrage, révèle les tendances les plus marquantes des recherches récentes, vers: l'évolution des comportements sociaux et leurs mécanismes, les relations avec l'environnement, l'histoire naturelle et sa diversité, enfin la biologie moléculaire. D'autres thèmes, jadis développés, ont presque disparu, de nouveaux émergeront demain..

The International Union for the Study of Social Insects (IUSSI) was created almost half a century ago by a handful of determined European researchers, particularly French and German. Today, the Union includes one thousand members and the Congress of Paris will constitute a new step in its development, as it will incorporate researchers from the former Soviet Union and from China.

The constant evolution of IUSSI indicates not only the interest of biologists for insect societies, but the impact of these insects on natural or modified ecosystems.

The content of the XII Congress of IUSSI, summarised in this volume, reveals the main trends of recent research: evolution of social behaviour and analysis of its mechanisms, the relationships between insect societies and their environment, life history and biological diversity, and finally molecular biology. Other themes which were previously well developed have disappeared this time; new ones will emerge tomorrow..

CONFERENCES PLENIERES

PLENARY LECTURES

REGULATION OF DIVISION OF LABOR IN HONEY BEE COLONIES: INTEGRATED HORMONAL, GENETIC, AND NEURAL ANALYSES OF SOCIAL BEHAVIOR

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"Research at one level (of biological organization) provides correction, constraints, and inspiration for research at other levels (1)." This dictum, written in reference to studies of the human brain, applies equally well to studies of other complex biological systems, such as insect colonies. Our understanding of the regulation of division of labor in an insect society has benefited from a synergism generated when analyses of higher-order patterns of colony behavior are integrated with analyses of mechanisms of individual behavior.

It has long been recognized that adult workers in some insect societies are capable of responding to changes in colony conditions by showing plasticity in age polyethism. A flexible system of division of labor presumably is very important to colony fitness, given that insect colonies develop and produce reproductives despite constant changes in environmental (external and colony) conditions. But the mechanisms that permit plasticity in worker behavioral development are only beginning to be understood. This question, like other similar questions related to the integration of activity in an insect colony, is compelling because it seems unlikely that any individual in a colony of highly eusocial insects has the cognitive capacity to acquire and integrate information on the global state of its colony.

Hormonal analyses of honey bee behavior have provided a firm foundation for mechanistic analyses of division of labor (2). These studies indicate that juvenile hormone (JH) is involved in the regulation of both age polyethism and responses to changing colony conditions. Genetic analyses of honey bee behavior (3) have similarly provided important information on plasticity in age polyethism. A genetic component to several aspects of division of labor has been demonstrated, including plasticity in age polyethism. A key result from a recent genetic study (4) is that differences in plasticity in age polyethism are due to differences in the rate of worker behavioral development; this linkage again suggests that there are common factors that regulate both processes.

These results were used to examine how bees obtain information on changing colony needs that results in

plasticity in age polyethism. We used two new experimental paradigms inspired by developmental biology, because workers, like cells, differentiate in response to local stimuli in ways that are appropriate at the global level. Results from both an analog of "cell culture" (bees reared outside of colonies in different sized groups in the laboratory) and "transplant" assays revealed that worker-worker interactions influence endocrine and behavioral development (5). These findings led to the formulation of the "activator-inhibitor" model for the regulation of behavioral development in honey bees (5). According to this model, a worker's rate of behavioral development is determined by an interplay between JH, designated as an intrinsic activator that promotes behavioral development, and an "inhibitor", an as-yet unidentified factor(s) transferred among workers that retards development. The model also specifies that the production of JH and the inhibitor are coupled, with older bees producing or transferring higher levels of inhibitor than younger bees.

Support for this model comes from the results of recent experiments. In colonies with precisely controlled age structures, we manipulated the opportunity for young bees in a focal cohort to interact with older bees and then determined behavioral or endocrine development. Precocious foraging was induced in the focal cohort by depleting colonies of foragers, but depleting an equal number of bees of all ages from otherwise similar colonies had no such effect. Delayed foraging was induced in the focal cohort by confining the foragers to their nest with simulated rain. Finally, we induced "hormonal reversion", i.e., a drop in JH from high, forager-like, levels to low, "nurse-like", levels, in the absence of brood, just by removing all the young workers. These results suggest that rates of behavioral development are strongly influenced by changes in patterns of social interaction, which presumably reflect changes in exposure to inhibitor. Preliminary findings (6) indicate that the inhibitor is not a highly volatile chemical or a sound, but may be a chemical or behavior associated with antennation and/or trophallaxis.

Important questions for future study are whether there are other factors that influence plasticity in age polyethism (queen, brood, climatic conditions, etc.), and if so, whether they exert their effects independently or through changes in worker-worker interactions and the hypothesized activator-inhibitor mechanism. One possible limitation of the activator-inhibitor model is that it currently is based mostly on results from the laboratory or very small colonies; more studies with larger colonies

are needed to test the robustness of the model. Nevertheless, in addition to providing a heuristic foundation for future work, there are important implications of the activator-inhibitor model for our understanding of colony organization. First, this model shows how a complex pattern of colony behavior can emerge from simple, deterministic, interactions among workers. Second, it predicts that the "normal" rate of behavioral development is not a consequence of a fixed ontogenetic program, but is determined instead by colony age demography and social interactions, as are the more atypical patterns of behavioral development observed under more atypical colony conditions. Third, it suggests that inhibitory social interactions are responsible for prolonging the within-nest phase of a worker's life, which is precisely the phase that has been elaborated upon most dramatically in the evolution of age polyethism.

Neuroanatomical analyses have provided new insights into the process of honey bee behavioral development and its regulation by JH. There is a reorganization of the mushroom bodies that is temporally correlated with the behavioral transition to foraging, even when individuals are induced to become precocious foragers (7). The volume of the Kenyon cell body region decreases while the volume of the neuropil increases. It is likely that this reorganization results in an increase in the "synapse to neuron" ratio, but cellular analyses have not yet been performed. Given the prominent role that the mushroom bodies play in insect learning and memory, these results suggest that neuroanatomical changes support the shift from the performance of simpler within-hive tasks to more complex foraging activities. The specific neurochemical and molecular genetic changes associated with this neuroanatomical reorganization are being actively pursued.

One possibility is that mushroom body reorganization is mediated by increasing levels of JH. Bees that received JH analog treatment but were confined to their colony showed the same neuroanatomical changes as do foragers (8). One way in which JH may regulate honey bee behavioral development is by exerting an "organizational" effect on the plasticity of the adult mushroom body, similar to the effects of gonadal steroids on brain and behavioral development in vertebrates. Exposure to high levels of JH would permit (although not necessarily independently trigger) the reorganization of the mushroom bodies and the subsequent onset of foraging.

This work illustrates strikingly the potential of the honey bee and other social insects as models for mechanistic studies of complex social behavior that occurs naturally within a readily discernible ecological context.

Comparative studies that determine the generality of the mechanisms identified in honey bees will assist the elucidation of both the mechanisms and evolution of colony organization. A causal role for JH in the regulation of age polyethism has been demonstrated for *Polybia occidentalis* wasps (9). A genetic component to the division of labor has been shown in several ant species (1). In an intraspecific comparative analysis, it was found that mushroom body reorganization also occurs in honey bee queens in the absence of flight experience (10). This demonstrates that mushroom body reorganization is not caste-specific in honey bees and is associated with more general aspects of behavioral development. Further analyses of regulatory mechanisms in honey bees and other species will deepen our understanding of insect social organization.

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SOCIAL INSECTS AS CENTRAL PLACE NAVIGATORS: EGOCENTRIC OR GEOCENTRIC SYSTEMS OF REFERENCE?

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Central-place foragers like social hymenopterans which depart from and return to fixed positions in their environment can resort to two principally different ways of navigation by using either *egocentric* or *geocentric* systems of reference. In the first case positional information is obtained by dead-reckoning (route integration), in the second case, the animal is expected to use the mental analogue of a topographical map. Rather than relying on information continuously collected *en route* (dead-reckoning), an animal using a geocentric system of reference can episodically take a positional fix, i.e. rely on information collected *on site*.

In social hymenopterans like bees and ants dead-reckoning is the predominant mechanism of navigation, but there is still substantial debate about the extent to which map-based information is used as well. All present data on this subject can be explained sufficiently by assuming that foraging bees and ants rely on path integration and site- or route-specific landmark information. There is no need yet for invoking the concept of a mental map.

THE EVOLUTION OF EUSOCIALITY

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Eusocial insects are defined as those that show cooperative brood care, reproductive caste differentiation and overlap of generations. I argue that this definition is rather restrictive and has often prevented the simultaneous consideration of somewhat less social insects and cooperatively breeding birds and mammals which exhibit levels of altruism comparable to that exhibited by many eusocial species of bees and wasps. I suggest therefore that the definition of eusociality be broadened to permit the inclusion of all species showing substantial levels of altruism towards group members (Gadagkar, 1994).

The evolution of eusociality has two components, the origin of eusociality - concerned with the conditions under which altruists can invade a population of selfish, solitary individuals and the maintenance of eusociality - concerned with the conditions under which selfish mutants cannot invade a population of altruists. Hamilton's inclusive fitness theory provides a powerful unifying framework to explore both the origin and maintenance of eusociality. However, the problem of the maintenance of eusociality is not as easily amenable to investigation because it may simply be difficult for mutations to take highly eusocial species back to the solitary, non-social condition. As for the origin of eusociality, the inequality in the inclusive fitnesses of workers and solitary nest builders may be brought about by a number of factors leading to genetic, physiological, ecological and demographic predispositions to eusociality.

Genetic predisposition implies that workers have access to more closely related brood than solitary foundress do. Physiological predisposition implies that workers are less fertile compared to solitary foundresses. Ecological predisposition implies that due to the advantages of group living, workers are more productive than solitary

nest builders. Demographic predisposition implies that demographic factors such as mortality rates and time taken to attain reproductive maturity affect workers differently than they do solitary foundress.

I have explored the possibility of each of these kinds of predispositions in the primitively eusocial, old world, tropical polistine wasp *Ropalidia marginata*, a model system that appears to be especially suited for the purpose. My conclusion from these investigations is that while *Ropalidia marginata* has little or no genetic predisposition, it has significant extents of ecological, physiological and demographic predispositions to the evolution of eusociality.

In addition, two general conclusions emerge from these investigations. The first has to do with the role of developmental plasticity in social evolution. I argue that not only will demographic factors like time taken to attain reproductive maturity make it worthwhile for some individuals to assume queen-like roles and for others to assume worker-like roles, but also that such demographic factors will coevolve with eusociality (Gadagkar, 1991). For example, late reproducers in a eusocial species will have a smaller selective disadvantage compared to those in a solitary species because of the possibility of gaining indirect, social fitness in the former. What this means is that one can also envisage the evolution of highly eusocial species starting from solitary ancestors through selection for developmental plasticity. In a solitary species, any character such as time taken to attain reproductive maturity, ovary size, mandible size etc., will have limited developmental plasticity because both queen and worker functions will have to be optimized under a single developmental programme.

As the worker-like individuals begin to rely increasingly on the social component of inclusive fitness and the queen-like individuals continue to rely on the direct, individual component, I speculate that there would begin quite a different regime of selection. There would be a relaxation of stabilizing selection on genes that regulate the making, in workers, of structures and

behaviours needed only in queens. Conversely, there would be a relaxation of stabilizing selection in queens, on genes that regulate the making of structures and behaviour needed only in workers. This should make possible, previously impossible levels of directional selection in workers, on genes that regulate the making of structures needed for workers and in queens on genes that regulate the making of structures needed in queens. In a process analogous to evolution by gene duplication,, genes needed in workers and in queens can evolve to new and extreme levels because worker and queen developmental programmes need no longer be optimized in the same individual.

The second general conclusion concerns the direction of social evolution. The inclusive fitness models I have developed to test the role of demographic factors in the evolution of eusociality are completely symmetrical with respect to whether the worker is fitter or whether the solitary foundress is fitter. Only the values of the parameters in the models will decide which is fitter. What this means is that evolution should be able to move both from the solitary to the eusocial as well as from the eusocial to the solitary. The evolution of solitary life or selfishness from the eusocial condition or the process of reverse social evolution as it may be called, has seldom been considered and never been adequately documented and it may truly be rare. It is significant however that the cape honey bee has evolved thelytoky, permitting workers to produce female offspring. Perhaps even more significant is the fact that in many ponerine ants, workers mate and reproduce and may rear no queens at all. These examples, however limited, I argue, can be used as model systems in the study of reverse social evolution.

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LIFE HISTORY EVOLUTION: THE ROLE OF THE PHENOTYPE IN EVOLUTIONARY THEORY.

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The analysis of life history evolution has advanced evolutionary and behavioural ecology, but it has also clarified evolutionary biology in a more general way. The local advances include quantitative predictions of major features of life cycles, such as age and size at maturity, clutch size, and reproductive investment. They also include explanations of major puzzles, such as senescence and interspecific variation in lifespan. These advances will be briefly reviewed and illustrated with examples drawn from the evolution of phenotypic plasticity and from the role of tradeoffs in the evolution of senescence. Life history evolution also suggests two important general roles for the phenotype in evolution: phenotypic variation among individuals in life history traits is the mechanism of natural selection, and the plasticity and canalization of the phenotype mediates the expression of genetic variation in ways that strongly influence the response to selection. These general roles of phenotypes will be illustrated with the evolution of canalization of life history traits and with the analysis of genetic variation for reaction norms. Applications to social insects will be discussed.

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SYMPOSIUM

SYMPOSIA

BEHAVIOURAL ECOLOGY OF STINGLESS BEES (APIDAE, MELIPONINAE)

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Introduction

The stingless bees (Apidae, Meliponinae) form a group of tropical bees of great ecological importance in the humid and dry tropical forest. Hundreds of species demonstrate interesting differences in body size, the use of nesting substrates, food selection, and foraging recruitment systems.

The regional distribution of the species is of ecological interest. There are many sympatric species in certain regions: some species have a large distribution area, while others have a very restricted distribution. Limited information is still available about the behavioural ecology of these bees. Roubik (1989) compiled the available information in his book on the ecology and natural history of tropical bees. This author also studied the ecological adaptations of species in various parts of the neotropics. Comparing the reviews by Sakagami (1982) and by Engels & Imperatriz Fonseca (1990) it appears that few publications were recently added about reproduction and behaviour of sexuals. Few data are still available about colony multiplication, although reproductive behaviour, at the level of individual bees and at the level of the colony, has received some more attention recently. Previously Sakagami and a number of Brazilian co-workers have published an impressive series of papers on the behavioural organisation of the typical mass provisioning system of larval feeding through the rapid provisioning and oviposition process (POP) in various stingless bee groups. Japanese and Brazilian investigators continued this line of research.

The intriguing systems of communication concerning food collection have hardly been studied after the publications by Lindauer and Kerr (1958) and by Esch et al. (1965). Only recently some papers were published about this topic (Pereboom and Sommeijer, 1993; Kerr, 1994).

Sommeijer and De Bruijn recently published a review about the intranidal feeding systems and trophallaxis behaviour in stingless bees and raised the discussion about the evolutionary origin of the typical temporal structure of POP.

In this symposium various aspects of the behavioural ecology of stingless bees will be discussed and special attention will be given to the adaptation of the characteristics.

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BEHAVIOR AND EVOLUTION OF *TRIGONA*

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By assembling data from field studies and museum specimens, I used a parsimony algorithm and the 'consensus tree' method to deduce which biological characteristics may resemble ancestral *Trigona*, which are evolutionary innovations, and which features have evolved independently in various taxa. Selectively ignoring either behavioral or morphological data seriously impaired analysis of the genus. Data on male morphology and correct association with workers, in particular, permitted appreciation of taxonomic groups and valid species names. There are 27 *Trigona* s. s., all Neotropical, taking into consideration four undescribed species and five new synonyms. Basic species groups are reduced to 15 by considering the 13 traits I analyzed, 8 morphological and 5 behavioral. Foraging, nest construction and nest defense behavior provided most of the insight for recognizing groups among *Trigona* sensu stricto. Morphological data yielded apomorphies (which help define groups) about half as often as did behavioral traits. Behavioral lability through evolution was demonstrated in choice of nest material, nest site and nest defense behavior. The *T. fuscipennis* group (3 species) apparently switched to nesting within termite nests from ancestors that built aerial nests. Mud, dung and plant fiber nest materials were apparently abandoned in favor of pure resin both in the *T. hypogea* group and by *T. pallens*. Worker nest defense behavior became relatively passive in *T. muzoensis*, *T. rufescens* and *T. hypogea* — the first two shifted to obligate nesting associations with exposed-nest-building termites, presumably from tree-cavity nesting. In contrast, obligate necrophagy and passive versus aggressive group foraging behavior showed no reversals. Aggressive foragers comprise all the *Trigona* except *T. cilipes* and the *T. fulviventris* group (2 species), which are apparently the most primitive. Several innovations in aggressive behavior separated these species from the rest, along with one morphological change that may explain much of *Trigona* evolution — the presence of three large apical mandibular teeth. These teeth help the 24 other *Trigona* to excavate hard nest substrates, defend nests from large predators, perforate tough floral corollas or anthers, and mine resin or sap from living trees. *Trigona* are the only bees that build paper nests from chewed wood pulp, and this innovation seemed to be recent, existing at least in *T. nigerrima* and *T. dallatorreana*, although the nesting habits of their closest relatives, *T. venezuelana*, *T. sesquipedalis* and *T. dimidiata*, are still unknown.

REPRODUCTION STRATEGIES AND FEEDING ECOLOGY OF STINGLESS BEES IN RELATION TO ENVIRONMENTAL PROBLEMS

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The complex social behavior of stingless bees and the typical mass provisioning system of larval feeding through the rapid provisioning and oviposition process (POP) has led to specific processes of food processing, storage and broodcell provisioning. The typical temporal structure of POP has recently raised the discussion about its evolutionary origin. The adaptive significance of the rhythmic oviposition process of stingless bees was first hypothetically interpreted as a trait to support the reproductive dominance of the queen, and the evolution of temporary batched ovipositions in "integrated oviposition processes" could also be explained by this hypothesis. The evolution of the unique POP could also be interpreted as a result of natural selection processes. The mass provisioned broodcells in the nests of stingless bees and the storage of valuable pollen mass, pose a risk for exploitation by natural enemies. The specific behavior of larval feeding and oviposition enhances the protection of the valuable cell contents against pestlike phorid flies. In general the production of gynes is not seasonally restricted but occurs more or less continuously throughout the year. The typical mass provisioning of brood cells prohibits the use of "emergency queen cells" after accidental loss of the laying queen and replacement queens have always to be available. In most species, surplus queens are regularly slaughtered by the workers. Although some reports indicate the participation of males in various worker tasks, we found that the intranidal behavioural repertoire of males of *M. favosa* and *M. rufiventris* is very limited and that males are infrequently present and probably mostly in small numbers. We observed different laying workers in queenright *Melipona favosa* colonies: laying trophic worker eggs and reproductive worker eggs. In addition to the morphological differences of both eggs, there are distinct behavioural characteristics of the layers of TWEs and RWEs. This confirms that *Melipona* workers can be important for the production of males in queenright colonies. We will also discuss our first description of a large non-nest associated drone congregation area (DCA) of *Melipona favosa*. The about 400 drones originated from different nests. The males interacted aggressively. Olfactory stimuli triggered specific behaviours of the males as well as of the gynes. Gynes were attracted from distant nests and male aggression was evident but males do not immediately pounce on an arriving female (indicating mate-selection by the female?) The significance of this complex mating strategy for the male gene-flow will be discussed.

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REPRODUCTIVE STRATEGIES IN STINGLESS BEES GYNE MAINTENANCE IN THE COLONY.

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Meliponinae species evidence several ways of controlling gynes in the colony. Meliponini seems to be a homogeneous group concerning gynes origin and behaviour. Although many gynes hatch during all the year, they are killed as soon they become attractive. They can even live longer during short periods of colony's cycle. Refuges for many gynes are found in some species (*M. marginata*, *M. scutellata*). A polygynic species is known (*Melipona bicolor*). As a very diversified tribe, Trigonini bees have many possibilities for the gynes' control. The more common concerns to those species where gynes hatch mainly from royal cells, but rarely can be reared in worker-sized cells (*Nannotrigona*, *Plebeia*). The next step is related to those bees that often have dwarf, small, medium and seldom big sized gynes (*Schwarziana*). Another way for larvae from normal cells to become gynes is found in *Frieseomelitta* and *Leurotrigona*, where, in a short phase of colony cycle, several workers' larvae perforate nearby cell gaining access to an extra source of food. Some *Trigona* also controls the liberation of gynes in the colony. *Trigona spinipe* gynes are kept inside royal cells even if they are ready to go out. *Trigona recursa* and *Trigona hypogea* control the gynes' development inside royal cells which stay as quiescent pre-pupae until a colonial sign is given to complete ontogeny. As soon as attractiveness appears, most of Trigonini gynes are killed. For their maintenance in the colony, several control possibilities were described. Nevertheless, to be fertilized all of gynes need to be recognized and accepted for most of workers. This occurs as a result of supersedure or swarm.

EFFECTS OF WORKER REPRODUCTION ON SYSTEMS OF KIN RECOGNITION IN STINGLESS BEES

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Stingless bees are the group that is most diversified in the ritualized provisioning and oviposition process and in worker's reproductive oviposition at queenright colonies. There are five social systems of worker's oviposition. (a) Complete degeneration of ovaries and no possibility of oviposition even in queenless conditions (*Frieseomelitta varia*, *Trigona minangkabau*). (b) Production of males by workers occurs only in queenless colonies (*Leulotrigona muelleri*), like honeybees. (c) Workers produce eggs and the queen eats them before own oviposition. In *Melipona faciata*, workers lay eggs on food but it occurs outside the brood cell in *Nannotrigona* spp. In *M. faciata*, some (2 %) workers try to keep own eggs by closing brood cells after oviposition. The queen aggressively taps the closing workers. In a half cases, the workers succeed and in the rest cases other workers open the brood cells and eat the eggs. (d) Workers produce two different types of eggs. Eggs without nucleus (real trophic) are laid outside brood cells for the queen. Workers lay eggs with nucleus on food, sneakingly in cell-closing after the queen's oviposition in *Scaptotrigona postica*. A single brood cell receives one egg of the queen and a few eggs of workers and usually one of worker's eggs grows up. In *S. barrocoloradensis*, a worker lays an egg with nucleus on food and close the brood cell without no aggressive behavior by the queen and surrounding workers. "Peaceful" division of reproduction between the queen and workers is found in this species. (e) In the above examples all ovipositions occur in the provisioning and oviposition process but in some *Plebeia* a worker eats an own coming-out egg in front of the queen when it fails to escape from chasing by the queen. We hypothesize that these different contributions of workers to male production influence social systems in kin and nestmate recognition among workers. In species with high contribution of workers for male production, acceptance of a worker with a low degree of relatedness may reduce the inclusive fitness of the other workers due to loss of resources for rearing non-related offspring. However, in species with no possibility of worker's oviposition, such loss never occurs and contrarily labor of the accepted worker will contribute colony performance. To test this hypothesis, we compare systems of kin recognition in *T. minangkabau* (type a), *M. faciata* (c), *S. barrocoloradensis* (d) and others. In *T. minangkabau*, guards, patrolling in the nest, accept non-nestmate callows as often as nestmate callows, although guards recognize the difference. In *M. faciata*, the percentages of acceptance of introduced callows increase as a function of the degree of relatedness. Guards kill 47 % of non-nestmates and even 7 % of sisters. The average percentage of acceptance decreases when the invasion risk for the nest increases. Recognition is based on differences of cuticular hydrocarbon, which is basically determined genetically and in part modified by the colony odor after emergence. In *S. barrocoloradensis*, our hypothesis is not supported; guards accept even non-nestmate callows, as in *T. minangkabau*. A possible cause is colony conditions: male production occurs only in a specific season and in well-developed colonies. Our observation was done in a colony in which there is no male production by workers. We will discuss social evolution of stingless bees from viewpoints of systems of division of reproduction between the queen and workers and systems of kin recognition.

BEHAVIOUR OF MALES IN THE STINGLESS BEE
MELIPONA BEECHEII (APIDAE: MELIPONINAE).

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Marked males of *Melipona beecheii* were observed in colonies, kept in small observation boxes, using red light to avoid disturbances, in Guanacaste province (Costa Rica). Their behaviour was analyzed and found to be age-dependending. Young males spent most of the time in akinesis on combs with emerging brood (37%), "grooming" (34%) and walking around (27%). Older males spent significantly less time on grooming (18%) and akinesis (30%) than young males and significantly more time on trophallactic interactions and walking. Trophallaxis behaviour of males can be divided in interactions between males and receivings from workers. One third of trophallaxis was found to be with other males (N=76). Males were found to dehydrate nectar occasionally. No males were observed excreting wax.

Males stayed inside the nest until 19 days old on the average, and were never seen back once they flew out. Most males (90%, N=20) left the colony between 9 and 12 a.m. Males lived upto 74 days, averaging 45 days (N=7) in a closed hive.

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FOOD RECRUITMENT IN THE STINGLESS BEE, *MELIPONA EBURNEA*: COMMUNICATING LOCATION WITHOUT A SCENT TRAIL

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We studied the stingless bee, *Melipona eburnea*, on Barro Colorado Island, Panama, to learn more about its food recruitment abilities. This bee has also been known as *M. fasciata* and *M. rufiventris* in the literature, but neither name applies. It is the most common species of its genus in Panama and Costa Rica. Colonies contain from 500-800 adults and are found in rain forests under 1400 m in elevation. To study recruitment, we followed the method of Lindauer and Kerr (1958) by using identical paired feeders. We trained foragers from a colony in an observation hive to one feeder and monitored both feeders for the subsequent arrival of newcomers. The relative position of the two feeders was changed to test for recruitment to the correct direction, distance, and canopy level. A 40 meter canopy tower located inside the forest was used to examine canopy level recruitment. In all experiments, we repeated our trials after switching the positions of the control and experimental feeder to eliminate site bias. We found that *Melipona eburnea* can accurately recruit to a food source at a specific location. Newcomers arrive at the correct (1) direction, (2) distance, and (3) canopy level. To test for the possibility that foragers lay a scent trail, we placed the colony on the shore and trained bees to a feeder 100 meters over the water. Both control and experimental feeders were placed on the opposite shore, equidistant from the colony but 10° apart. Significantly more newcomers consistently arrived at the experimental feeder. A scent trail is evidently unnecessary. Analysis of videotaped behavior inside the hive reveals that the forager produces pulsed sounds (air-borne component recorded) while visibly vibrating her wings after returning from a good food source. She is attended by other bees who cluster and hold their antennae around her, following her as she makes rapid clockwise and counterclockwise turns. Some locational information may be encoded in such behavior inside the hive. However, foragers may also directly lead newcomers to the food source. Further experiments are planned to test for such piloting.

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POLLEN FORAGING MECHANISM OF *MELIPONA* STINGLESS BEES

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A study of the foraging behaviour of *Melipona beecheii* and *Tetragonisca angustula* revealed a remarkable difference in the daily pattern of pollen collecting, whereas patterns of nectar collecting were found to be rather similar. *Melipona* bees harvested 50% to 70% of their daily pollen amount before 8 AM. They start foraging before sunrise and many of the foragers leave the hive before the first bee returns. A second group of foragers starts foraging right after the return of the first returnee carrying pollen. This pattern could not be explained completely in terms of scout-recruit systems. We therefore developed a model in which individual motivation is regulated by previous experience in combination with information on availability of pollen sources obtained from the first returnees. This resource information is essential at the start of the foraging career and also after a drop in motivation due to unsuccessful flights. The model predicts that 1) the probability that a bee will continue foraging is positively correlated with its success on the previous flight (where success is a combination of load size and time spent foraging); and 2) that the successful bees of day one will be among the first to leave on day two, before new information on resources comes in. The unsuccessful foragers will need new information to raise their motivation above the threshold to leave the hive. Observation of individually marked bees revealed that 85% of the bees that carried average or large pollen loads continues foraging, whereas only 30% of the bees that carried a small pollen load continued. These data support prediction 1. Our results from colony level observations on *Melipona fasciata* demonstrate that a strong positive correlation exists between the percentage of 'successful' (= average to large) loads on day 1 and the number of bees and the rate at which these bees are leaving the next morning before new information on pollen sources is available. So far the model serves to explain most of the very characteristic early morning pollen foraging pattern of *Melipona* bees.

BIODIVERSITY AND SOCIAL INSECTS: AN INTRODUCTION

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This symposium will concentrate on ants and termites. We hoped to find some common ground between the invited papers and felt that we could not begin to consider the fascinating contributions made to biodiversity by bees and wasps, in the limited time available. Ants and termites exhibit many similarities. All are eusocial, with species or species groups that have evolved very different ways of using the same environment, leading to high levels of coexistence as well as competition between species. They are ground dwellers and this makes it much easier to recognise and catalogue the large impacts they have upon soils, vegetation and other fauna in the vicinity of their nests. Termites are mostly restricted to tropics and sub tropics whereas ants are found worldwide. Different problems are faced in both ecosystems. The main threat in tropics is the loss of primary habitat and the maintenance of the biodiversity and sustainable development. In temperate zones, much primary habitat is already lost and the main concern is the relationship between diversity and human activities. In this symposium, termites are used mostly to illustrate problems associated with the tropics and ants to illustrate problems associated with more temperate environments.

First, Lepage will illustrate the concept of functional groups and keystone species in termites and show the consequences in ecosystem stability and dynamics (soil organic matter recycling and forest-savanna boundaries). Then Bignell will illustrate how the termite communities are characterized in several forest ecosystems, from primary to highly perturbed and the likely effect of forest clearances. Bagine will look into more detail on the meaning of termite diversity within a genus along biogeographic zones. Noirot will round off examining evolution of termites and the consequences of symbiosis associated with them in the termite biodiversity.

Then turning to the temperate zone, Kipiatkov will give an outline of ant diversity in northern temperate zone, including the functional processes that enable ants to use these fluctuating environments. Gallé will take this up and examine community processes that occur in secondary cultural habitats that have been created by man. In much of the Old World these habitats have been in existence for a considerable time. Majer continues this theme by looking at the way in which the diversity of Australian ant communities is affected by man's activities. Apart from their role in altering and interacting with many other plant and animal species in their communities, social insect colonies themselves form habitats that can be exploited by other species. Elmes illustrates the importance of this in maintaining secondary biodiversity. Finally, little thought has been given to the conservation of social insects which have primarily been thought of as pests in many parts of the world. This is presently being remedied and Agosti will discuss this and emphasize the dominant position of social insects in the biosphere.

TERMITES BIODIVERSITY IN TROPICAL ECOSYSTEMS

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Social Insects as a whole, and mainly ants and termites, hold a dominant position in most tropical ecosystems, as compared to other heterotrophs, through their biomass and their great influence on soils and vegetation. Under the tropics, termites are the main decomposers in exploiting the large resource constituted by plant structural polysaccharides. This resource could be considered as a bottleneck in the detrital food chain owing to enzymatic barriers. Termites by-pass this difficulty through their evolved symbiosis with microorganisms (Protozoa, Bacteria, Fungi). Segregation between the little more than 2 200 known termite species is based on the different aspects of their life history traits: cast polymorphism, nest building and position, food regime and digestive capabilities, feeding and reproductive strategies. Data available for Africa illustrate that the communities are clearly structured by the climatic conditions represented by the rainfall/vegetation gradient at the regional scale. At the local scale, termite diversity goes with the habitat diversity together with some stability (with time) of the biotope. Moderately disturbed ecosystems often exhibit more termite species diversity than highly disturbed or no disturbed ones. Clearly, biotopes are saturated with numbers and biomass, as related to food available, rather than saturated with species numbers, as two biotopes with the same available energy (as litter) support similar termite biomass but exhibit very different diversity indices. Assemblage of species are described from several African tropical forests and savannas ecosystems and the meaning of functional groups is discussed in the case of termites species sharing a same resource. Illustration is given of termite functional groups in organic matter recycling in savanna ecosystems. Lumping species will depend to the process involved and to the degree of accuracy requested. Discrimination could be roughly done between humivorous and fungus-growing functional groups, or distinction could be more accurate within each group (ie consumers of fresh/old organic matter in the humivorous group, consumers of above/below-ground litter in the fungus-growing termites). Related to the concept of functional group is the thinking that some redundancy exist between the termite species within a functional group. The consequence being the dominance of few or one termite species in most anthropogenic environments (ie in industrial fields). Keystone species concept applied to termites is then discussed. A keystone species may be considered as a functional group with no redundant representation. Example is given of large earth-movers, as the mound-builder genus *Macrotermes* in African savannas. Such species create peculiar soil conditions that persist in their nests. Termite mound locally modify soil physico-chemical properties through the building activities. Modification of water dynamics and organic matter status result in a local increase in tree density and tree diversity. Termite mounds may form refugia for trees in a grassland and participate in the long-term dynamics of dry forests. After the termitaries have been abandoned by their builders, soil macrofauna (earthworms and hypogeous termites) colonize them, in higher densities than in the surrounding savanna. Consequences of this heterogeneity caused by termitaria in ecosystem functioning are discussed at different scales: the balance between the immobilization and mineralization of the soil organic matter and the dynamics of the forest-savanna boundaries.

THE DIVERSITY OF TERMITE COMMUNITIES IN A HUMID TROPICAL FOREST

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Termites were sampled in 1992 and 1993 by rigorous quantitative methods from five sites in the Mbal Mayo Forest Reserve of southern Cameroon. The sites represent a gradient of disturbance from light (near primary forest) to very severe (complete clearance by bulldozer), also including secondary woodland, forest plantation and farm fallow (manual clearance). The whole assemblage was very diverse (110 spp. of which approx. 30 are new species and 3 new genera), with a tendency for soil-feeding forms to dominate in forested sites. Abundance and diversity were greatest in sites of intermediate disturbance, but biomass was greatest in the near primary site. Abundance and biomass were reduced in 1993, but diversity remained high. Preliminary measurements of CO₂ and CH₄ fluxes from species representative of each functional group within the assemblage (provisionally 12 groups) suggests that carbon flows through termite decomposer communities are relatively and absolutely greatest in undisturbed sites. Severe stress to the ecosystem greatly reduced termite diversity and may change the balance of activities within the decomposer community as a whole.

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BIODIVERSITY OF THE TERMITE GENUS *MACROTERMES* IN KENYA: TAXONOMY, DISTRIBUTION, DENSITY PATTERNS, AND INTRASPECIFIC VARIATION

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The fungus growing termite genus *Macrotermes* is common in most areas of Kenya and builds conspicuous open or closed mounds. Currently, the taxonomy recognizes five species: *M. bellicosus*, *M. falciger*, *M. herus*, *M. michaelsoni*, and *M. subhyalinus*. The taxonomic status is uncertain for three additional populations which build characteristic mounds. We investigated this difficult taxonomy of *Macrotermes* in Kenya by morphometric and by biochemical techniques, e.g. allozymes and cuticular hydrocarbons. These methods clearly recognize one further species previously referred to as *M. subhyalinus*. Tentatively we name this species "*M. jeanneli*". Furthermore two species (currently assigned to *M. subhyalinus* and *M. michaelsoni*) appear to have been identified incorrectly. The *Macrotermes* fauna in Kenya assembles species from four biogeographic zones: *M. falciger* within the coastal strip, "*M. michaelsoni*" and "*M. subhyalinus*" from the southern tropics, *M. bellicosus* and *M. herus* from West Africa, and "*M. jeanneli*" from the dry northern tropics. The mound density within the distribution range of a species is quite variable and ranges up to 4 mounds ha⁻¹. On a large scale, density correlates with climatic factors and with soil types. Distributional borders are sometimes characterized by an abrupt decline of density without obvious environmental correlates. Within distributional areas, *Macrotermes* colonies occur in a clumped pattern either caused by small scale environmental heterogeneity or by the dispersal strategy of a species. In contrast to other investigated *Macrotermes* species, hydrocarbon profiles of *M. falciger* and "*M. michaelsoni*" show a high intraspecific variability, which may point to a not yet understood diversity within the same area. At least within "*M. michaelsoni*" this pattern is not caused by intracolony variation or by seasonal and annual influences. This diversity suggests the existence of "intraspecific" sympatric types of uncertain taxonomic status. In addition, within the biogeographic zone of the coast at least two allopatric types of distinct closed mounds exist, which are as yet assumed to be built by the same species "*M. michaelsoni*". So far our approaches do not separate these populations. The different mound types, however, may indicate genetic heterogeneity within one species or the occurrence of different species. Such intraspecific variation should be considered in biodiversity studies. Both, intraspecific variation as well as the conjunction of several biogeographic zones within a limited area make Kenya to a hot-spot in biodiversity of termites.

EVOLUTION of SYMBIOSIS and BIODIVERSITY in TERMITES

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The termites, with 270 described genera, form a very homogeneous order both morphologically and by their type of reproduction. Their evolution has been very constrained by their food (dead vegetal matter made of ligno-cellulosic material) the digestion of which is assisted by complex symbiotic associations. The diversification of termites is linked to changes in symbiotic interactions permitting access to more diverse food sources. The first dominant symbionts were intestinal cellulolytic Flagellates which are still present in 6 out of 7 families (but only 17 % of extant genera). Primitively, the nest is dug within a piece of dead wood giving both food and shelter, but from which the small colony cannot escape. The Termopsidae and Kalotermitidae (10 % of genera) have remained at this stage. A first evolutive leap was the settling of a network of underground galleries extending the foraging area outside the nest proper. Simultaneously, a true worker caste differentiated, but both changes were probably polyphyletic, appearing independantly in Mastotermitidae, Hodotermitidae, Rhinotermitidae and Termitidae. The next jump was the loss of the symbiotic Flagellates (family Termitidae : 83 % of extant genera) which allowed new symbiotic interactions with many types of bacteria. Although the role of these bacteria remains poorly understood, they permit the utilization of more diverse food, especially the litter at different stages. Particularly important is the exploitation of the humic substances of the soil, a diet adopted by 63 % of the genera of Termitidae (53 % of the total). Finally, another step occured in the Macrotermitinae through their mutualism with the fungus *Termitomyces*. Although morphologically less diverse (only 13 genera or 4,8 % of the total) this subfamily is highly successful in tropical Africa and Asia, with many key-species in most ecosystems.

SEASONALITY AND BIODIVERSITY OF ANTS IN THE NORTH TEMPERATE ZONE

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The species diversity of ants in North Palaearctic (including forest and more northern zones) is fairly restricted. In fact there are only five taxonomic groups of ants living in this region: the genera *Formica*, *Lasius*, *Myrmica* and the subgenera *Camponotus s. str.* and *Mychothorax*. The aim of our work is to reveal the eco-physiological characteristics of these boreal ants that distinguish them from more southerly distributed groups and allow them to inhabit the north temperate zone. Boreal ants use two main strategies of adaptation to the temperate climate. First, most of the species have the annual cycle characterized by the stable winter diapause of queens and larvae and the hibernation with diapausing larvae (the so-called cycle of *Myrmica* type). This strategy permits them: (1) to feed larvae from the early spring to the late autumn thus using more effectively the whole warm period of the year; (2) to extend the development of larvae to two or even three summer seasons. Secondly, the species of the genus *Formica* have another type of annual cycle: only the queens enter diapause in autumn and ants, therefore, hibernate without the brood. This strategy can only be appropriate for boreal ants in a combination with the very rapid brood development allowing them to rear sexuals and new workers from the eggs during a short warm season. All *Formica* species studied have developmental rates that are about twice greater than in *Myrmica*. We consider this trait as a preadaptation to the boreal climate because the other species of the tribe *Formicini* (e.g. *Cataglyphis*) all distinguished by *Formica* annual cycle type but more southerly distributed have exactly similar rates of development. All boreal ants are characterized by rather low temperature thresholds of development (less than 15°C) as compared with more southern species whose development is only possible at the temperatures above 17 or even 20°C. In *Myrmica rubra* L. the temperature thresholds of development for eggs and larvae are found to be between 9 and 10°C near Belgorod (a. 50°N) and between 4 and 5°C in St. Petersburg region (a. 60°N). Such geographical variation of the temperature threshold values diminishing with the increase of the latitude is described for the first time in insects. We suppose this phenomenon exists also in other ant species. The temperature thresholds of ants with *Myrmica* cycle type are noticeably lesser (below 13°C) than in *Formica* species (about 14-15°C) allowing them to develop the brood at the inferior spring and autumn temperatures. The optimal and preferred temperature ranges of most of boreal ant species are significantly lower in comparison with southern ants: between 20 and 24°C in *Myrmica* and *Lasius* and about 25°C in *Formica*. It is interesting that *Camponotus s. str.* and *Mychothorax* species have substantially higher thermal optimums and preferendums (about 27-28°C). The existence of these ants in boreal regions is only possible owing to the effective exploiting of the daily rhythms of temperature in their exposed nests.

STRUCTURAL TRENDS OF ANT ASSEMBLAGES IN A SUCCESSIONAL GRASSLAND UNDER STRESS AND PERTURBATION

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Ten years' study was performed on the composition, diversity, structure and dynamics of ant species assemblages in a sandy grassland of patchy character. Close correlation was observed between the information content of the habitat utilization and that of the temporal occurrence of the studied ant species. A bimodal pattern in the combined spatio-temporal information measures indicates that the ants can be grouped in two i.e. generalists and specialists. There is a possible correspondence between this bifurcation and the core-satellite species theory. Secondary succession after ceasing grazing led to a small-scale spatial differentiation and three main coalitions of species can be identified on the basis of their spatio-temporal coexistence. The drought-induced stress, however, resulted in a homogenization in the second part of the study period, which is well demonstrated by the topographic pattern transformation of the points representing the sampling sites in the PCoA factor space as well as by the changes in the dendrograms which classify ant assemblages. A temporal autosimilarity analysis revealed that the high diversity ant assemblages of small habitat patches are less persistent and more exposed to environment-induced changes. The community-level response to experimental disturbances (watering, grazing, trampling, vegetation cutting, removal of upsoil) is effect-specific in ants.

CHANGES IN WESTERN AUSTRALIAN ANT BIODIVERSITY AS A RESULT OF VARIOUS LAND USE PRACTICES

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Although by world standards Western Australia is a relatively undeveloped region, considerable areas of native vegetation have been modified by pastoral-cropping, rangeland-grazing urbanization and mining. Ant diversity is reduced and community composition changed by each of these land uses. Pastoral-cropping has the greatest long-term effect on ant diversity, followed by urbanization, mining and rangeland-grazing. In this paper we present data on the extent of these various land uses in each major Western Australian vegetation association. Then, examples of ant diversity and community composition (see references below) for each land use are coupled with GIS information on the extent of each land use in the various vegetation associations to calculate indices of "biodiversity quality" for each vegetation association. The findings relate to Australia in general and may serve as a framework for estimating losses of biodiversity in other countries and continents.

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SOCIAL PARASITISM AND BIODIVERSITY: THE EXAMPLE OF MACULINEA BUTTERFLIES.

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For more than 30 million years social insects, particularly ants, have been a dominant force in the environment at the scale at which they live. Cooperation and communication between individuals make them efficient foragers that can monopolise food resources, and formidable predators that can attack organisms many times their size. Consequently many plants and insects have evolved strategies to coexist with social insects; these range from avoidance through mutual tolerance and mutualisms to parasitism. The social insect community of any ecosystem therefore, has a direct effect on the biodiversity of the system. Social insect nests are usually strongly defended and are very dangerous places for animals that are not members of the society. On the other hand, any creatures that can fool a colony into tolerating them, find the nest to be both an haven from other predators and often a source of easy-living. In case of ants, there is at least one obligate inquiline species for every species of ant. Most species in the family *Lycaenidae*, which includes about one third of the world's butterflies, have evolved a relationship with ants. Generally, lycaenid caterpillars pay a tax in sugars and amino acids that they secrete from special glands, in return they are tended and protected from predators and parasitoids. Some species of caterpillars are even herded into the nest for safety at night, and brought out again to feed during the day. It is believed that this type of behaviour has led to the social parasitism shown by *Maculinea* butterflies. In Europe, the genus *Maculinea* comprises five species all of which are Endangered on a world scale. Each *Maculinea* species is a specialist parasite of a different species of *Myrmica* ant. Three species have evolved to be predators, once accepted into the nest caterpillars feed upon ant larvae. The other two species have evolved a cuckoo relationship, caterpillars beg food from the ants much in way as described for *Atemeles* beetles. Both lifestyles have led to many behavioural specialisations that greatly interest naturalists. Despite the protection afforded by the ants, each *Maculinea* species has an host-specific parasitoid species which have also evolved special behaviours to avoid the ants. The ant-butterfly-parasitoid relationships are used to illustrate the primary role of ants in maintaining biodiversity and highlight the problems associated with the conservation of such systems.

CONSERVATION OF PESTS?

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Social insects have a substantial impact on large parts of the world. In moist tropical forests they can comprise up to one third of the whole animal biomass and in several ecosystems they are one of the key players in such functions as pollinators, predators, seed distributor or intermediate hosts of a wealth of butterflies. But in environments used and under control of men, they cause huge damages to crops, to human infrastructure, to the cultural heritage, and due to human mobility, they have an often frightening impact on local faunas. Does such a vital group of animals deserve our conservational attention and efforts?

Few social insects species are known to be threatened. In these cases the classical approach of species conservation is still appropriate. These include ant species such as *Aneuretus simonii*, *Nothomyrmecia macrops* or the recently discovered *Adetomyrma venatrix* that are single representatives of phylogenetic lineages and restricted to threatenend, geographically very restricted habitats. Another case or the European wood ants (*Formica rufa* group) which, without protection, are threatened by over exploitation and forest management.

Just because of their dominant role in the biosphere, which can even cause huge losses or gains to world economy, social insects have a potential to contribute to the protection of the biosphere. This is further supported by their complex interaction with other organisms and physical environment. An understanding of their abundance and distribution could be used as an indicator for the distribution of biological diversity, or in the long term for global changes, i.e. social insects have a potential as monitor species. Thus, social insects should play a further key role, namely within recent efforts in modern conservation, management of our environment.

STUDYING SOCIAL INSECTS IN AN AGE OF MOLECULAR BIOLOGY

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Social insects fascinate us because of their sociality, their ecological dominance, and the ease with which they may be found. Tracing their sociality and morphology through time completes the evolutionary inventory. Much progress has been made with the tools of the recent past, allozymes, which are often still useful. But now we have a huge potential increase in precision because of the vastly larger quantities of data provided by molecular biology. Mitochondrial DNA allows the tracing of maternal lineages, and nuclear markers give us the power to not only determine how many males a particular queen has mated with but whether these males are related to each other. Genealogies of genes add new precision to biogeographic studies. For the larger view of social structure, these new tools should finally fulfill the genetic promise to analyse population structure with authority, e.g., providing definitive tests of unicoloniality on one case or the integrity of gamergate colonies on the other. Social insects are proving variable enough at the molecular level for the most demanding population biologist. Morphological phylogenies will be enhanced with the great flood of DNA sequence information just beginning; any disagreements of new with old pictures of social insect phylogeny can only yield illumination for all. Questions once silly to ask may now be considered. What are the genes responsible for polygyny in fire ants and in *Formica*, and are they the same? Is there a limit to how many sex alleles there can be, and what does the answer imply for sociobiology? Such questions once seemed presumptuous when all believed in the harmonious change of many loci in evolution; now most accept that single loci can be important. Perhaps soon single loci modifying the probability of eusocial behavior will be found, enabling us to study the actual workings of kin selection.

IDENTIFICATION OF THE HONEYBEE (*APIS MELLIFERA* L.) CHROMOSOMES WITH FLUORESCENCE IN SITU HYBRIDIZATION

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Fluorescence in situ hybridization (FISH) has been shown to be particularly sensitive in locating specific DNA regions on the chromosome (Korenberg et al 1992). Especially highly repetitive DNA is easy to detect. Beye and Moritz (1993) detected the heterologue of *Drosophila melanogaster* rDNA on two chromosomes in the honeybee (*A. mellifera*). Here we report on characterization of the honeybee chromosomal set using FISH and a set of high copy DNA probes and the rDNA of *D. melanogaster*. The ribosomal clone pD103 containing the repeated rDNA gene of *Drosophila* (Tautz et al 1988), a probe pSAM1 carrying a sequence of the reiterated *Alu* family (Tares et al 1993), and a probe pGC6 isolated by Beye and Moritz (1994) were used for FISH according to the technique described by Beye and Moritz (1993). Chromosomes were prepared from testes of drone larvae (stage L3-L4) according to standard techniques. Using FITC staining the preparations were analyzed under an epifluorescence microscope and documented with a CCD video camera and false color image analysis software.

If the chromosomes are subdivided in three size classes, each chromosome can be identified on the basis of size and a specific combination of FISH labels. Interpretational problems can arise if the chromosomes are too much condensed in the preparation. In such cases particularly chromosomes 8 and 9 as well as 15 and 16 may be difficult to identify. With increasing expertise of the observer, however, the chromosomal set can be interpreted even if the chromosomes are in a rather condensed form. This study is the first report on assigning genetic markers to chromosomes in the honeybee. We are optimistic, that this will form the methodological backbone for a swift physical mapping of the honeybee genome. Looking at the plentiful advantages the system honeybee offers for genetical questions, a physical linkage map will form an absolutely indispensable data basis to successfully continue genetic research on *Apis mellifera*.

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PUTATIVE OLFACTORY RECEPTOR GENES IN THE HONEYBEE *APIS MELLIFERA*

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Neural processing of general odors exhibits striking similarities in such phylogenetically distant species as mammals and honeybees, posing questions as to the evolution of olfaction. In the honeybee, the crucial role of the antennal lobe in odor coding and feature extraction has been extensively studied (Masson *et al.*, 1993). However, the molecular mechanisms underlying the construction of the peripheral odor image by receptor cells remain unclear. In vertebrates, the transduction of odors is accomplished by protein receptors which belong to the superfamily of seven transmembrane domain receptors, coupled to G proteins. The presence of G proteins and cyclic nucleotides in insects (Breer *et al.*, 1988) as well as in vertebrates suggests similar transduction mechanisms. In mammals, the protein olfactory receptors are encoded by a large multigenic family (Buck & Axel, 1991). Degenerate primers derived from sequence alignment of members of this family were used in nested-PCR amplification on honeybee antennae cDNA and a total cDNA library. Four putative odor receptor genes have been cloned. Their deduced amino acid sequences present noticeable similarities with those of vertebrates. A preliminary phylogenetic study suggests that they belong to three different subfamilies following the definition of Lancet and Ben-Arie (1993). Consequently, the seven transmembrane domain receptors may also mediate olfactory transduction in insects, and at least some of their genes are members of the same multigenic family uncovered in vertebrates.

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BIOGEOGRAPHY OF *APIS CERANA* BASED ON MTDNA SEQUENCE DATA

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This study examined *A. cerana* from Japan, Korea, Taiwan, the Philippines (Palawan, Luzon and Mindanao), Indonesia (Sulawesi), Malaysia (mainland and Borneo), Thailand, India (mainland and Andaman Islands), Sri Lanka and Nepal. As a source of characters, I sequenced a portion of the mitochondrial genome including a non-coding region found between the leucine tRNA and cytochrome oxidase II genes. The non-coding region proved especially informative for infra-specific biogeography, and revealed 2 major (widespread) and 4 minor (geographically restricted) lineages. One major group contains black bees of the Asian mainland (Korea, Thailand, peninsular Malaysia, Nepal and black bees of India), plus bees on those islands that were attached to the mainland during the Pleistocene, when sea levels were lower (the Japanese islands, Palawan, Borneo and black bees of Sulawesi). The non-coding regions in these bees are very similar, though the bees of Thailand, Malaysia, Borneo and Palawan share several unique base substitutions, and the black bees of India show the most intra-population variation of any group studied. The second major group includes the yellow bees of India, Sri Lanka and the Andaman Islands (*A. cerana* is reported to have been imported to the Andaman Islands from Bombay; Verma, pers. comm). The non-coding region was virtually identical in all of the yellow bees examined. The minor forms were found in isolated island populations. The bees of Luzon and Mindanao each have a unique non-coding region. The yellow bees of Sulawesi and the bees of Taiwan have lost most of the non-coding region, though the points of excision differ in the two groups, pointing to independent loss. The islands of Luzon, Mindanao and perhaps Sulawesi are believed to have remained isolated from the mainland during the Pleistocene; the highly divergent mitochondrial sequences of *A. cerana* on these islands could be due to gradual divergence during long periods of isolation, or rapid drift in relatively small populations. However, the island of Taiwan was most likely attached to the mainland during the Pleistocene. The divergent genome of the Taiwanese bees is perhaps attributable to drift alone. Comparative biogeographic studies are under way for dwarf bee and giant bee populations.

MACRO- AND MICROGEOGRAPHIC STRUCTURE OF A HYBRID ZONE FORMED BETWEEN THE TWO INTRODUCED FIRE ANTS SOLENOPSIS INVICTA AND SOLENOPSIS RICHTERI

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An extensive hybrid zone has formed between the two introduced fire ants, *Solenopsis invicta* and *S. richteri*, in the southeastern USA wherever these two species come into contact. We collected ants representing each of these two species and their hybrid from 550 colonies at 106 sites throughout Mississippi, Alabama, and Georgia, USA. Identities of each of these colonies were determined using informative allozyme and RAPD DNA markers in an effort to better understand the distribution of these two species and their hybrid. *Solenopsis richteri* is currently found only in northern Mississippi, *Solenopsis invicta* is found throughout the southern tier of Mississippi, Alabama, and Georgia, and these two species are separated by a large area of hybridization extending from central Mississippi to western Georgia. Furthermore, the data reveal a minor tail of introgression of alleles of *S. richteri* into *S. invicta* that most likely reflects the documented recent movement of this zone northward. To further determine what evolutionary forces are important for the structure and maintenance of this zone, samples of alate queens representing 1426 colonies were collected from 44 sites along two transects in central Mississippi spanning the entire width of the hybrid zone. A single queen from each colony was scored for eight informative allozyme markers, five morphological characters, and a single codominant RAPD DNA marker (one transect only) and these data were analyzed to determine whether selection against hybrids exists. We observed complete concordance between all types of markers along both transects. Such concordance argues against strong selection acting against hybrids at one or a few major loci. Furthermore, such concordance suggests either that no selection acts against hybrids or that there is selection against hybrids that it is spread uniformly throughout the genome. We invoke the latter hypothesis, based on two independent lines of evidence from previous studies suggesting some breakdown in the regulation of development of hybrids. The presence of selection against hybrids being uniformly distributed among many genes has important implications for speciation patterns in this group of ants, suggesting classical allopatric speciation with genetic differences accumulating gradually throughout the genome.

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MOLECULAR ANALYSIS OF RELATEDNESS IN
AGGREGATED HONEY BEE (*APIS MELLIFERA*)
COLONIES. DO OPPOSITES ATTRACT?

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Honey bee swarms aware of two nest sites of equal value tend to select the more distant site (Lindauer, 1955). Presumably, moving as far as possible from the natal nest reduces competition and the possibility of consanguineous mating. This tendency of swarms to select distant nest sites may explain why natural aggregations of *A. mellifera* have not been reported. However, in the related species *A. dorsata*, aggregations of colonies are common. A survey of the spatial distribution of feral *A. mellifera* colonies showed that they too can be markedly clumped, with up to 10 colonies $10,000 \text{ m}^{-2}$. For these heavily clumped colonies, we inferred queen genotype from worker samples for 1) malate dehydrogenase 2) a mitochondrial DNA length polymorphism 3) two microsatellite loci. Aggregations were composed of both related (ie originating from one colony), and unrelated colonies. Thus, swarms do not always travel far from the natal nest in an environment that is replete with nesting sites. Second, it seems likely that existing colonies attract swarms. We speculate that swarms may judge nest sites close to existing (successful) colonies as likely to increase survival by (a) informing the swarm that the environment has the floral resources to support a bee colony (b) ensuring more rapid mating for the swarm's future queens.

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THE PHYLOGENETIC RELATIONSHIP AMONG SEVEN ANT SUBFAMILIES: A MOLECULAR STUDY

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The phylogeny of ants (Hymenoptera: Formicidae) has been revised several times within the last 40 years; yet several inconsistencies remain—even at the subfamily level. The disagreements seem to result from a lack of objectivity; morphological and behavioural characters are chosen to suit the purpose with the poorly justified hope that changes in these characters reflect an evolutionary history without periods of convergent or reversed evolution. The present study concerns the basal structure of the phylogeny among ants (i.e., relationship among Formicinae, Dolichoderinae, Myrmeciinae, Ponerinae and two appropriate out group taxa, i.e. Vespidae and Mutillidae), the placement of Pseudomyrmecinae and Myrmicinae, and the placement of the living-fossil *Nothomyrmecia*. Using as data mitochondrial protein-coding DNA from the slow-evolving cytochrome *b* gene we analyse these phylogenetic questions by means of maximum likelihood, parsimony and bootstrap analyses. In agreement with two previous phylogenetic analyses of insect mitochondrial DNA^{1,2}, our study illustrates the great difficulty in obtaining conclusive answers to the phylogenetic questions. The reason for this difficulty is explained by means of directional mutation pressure³ which has increased the A+T content in insect mitochondrial DNA to levels never recorded among vertebrates⁴. The consequence of the high A+T bias (~90% at silent codon sites) is an increased likelihood of convergent evolution⁴. By increasing the DNA sequence data from each species and keeping the number of taxa low, and by removing those codon sites which are most affected by A+T pressure (i.e., third codon positions) from the phylogenetic analyses, we were able to improve the likelihood of obtaining conclusive answers to the phylogenetic questions on the evolution of ants. For example, with a subset of DNA sequence data, the basal structure of the phylogenetic tree suggests that Myrmeciinae was the first subfamily to diverge from Formicinae, Dolichoderinae and Ponerinae, and with Ponerinae diverging from Formicinae and Dolichoderinae at a later stage. However, this result is not yet significantly better than most alternative phylogenetic scenarios, implying that more DNA sequence data is needed. While this abstract is being prepared for publication, we will continue to obtain more DNA sequence data from the ants, and hope to present conclusive answers to the phylogenetic questions mentioned above.

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MICROSATELLITE ANALYSIS OF MATERNITY IN VESPID SOCIETIES

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Microsatellite loci consist of tandem repeats of short DNA motifs. They tend to have multiple alleles differing in the number of tandem repeats. They are found¹ by probing a library of genomic DNA with a synthetic oligonucleotide of the desired repeat motif. Positive clones are sequenced to confirm the presence of microsatellite repeats and to obtain flanking single-copy sequences for use in design of primers for the polymerase chain reaction (PCR). PCR can then be performed on tiny quantities of any individual's genomic DNA to obtain sufficient quantities of the DNA at the microsatellite locus to score on a gel. Because microsatellites are highly variable and codominant, they are very useful in estimating relatedness or in assigning parents.¹ Assignment of maternity in polygynous colonies is greatly facilitated by a trick; in addition to genotyping the offspring and putative mothers, we also genotype the sperm stored in the spermatheca of each mother.^{2,3} This can make maternity assignment very accurate even with only a handful of loci. A study of 9 foundress-stage colonies of *Polistes annularis* illustrates the possibilities. Nearly all foundresses were found to be singly mated, and the mates of foundresses on the same colony were unrelated. Progeny assignment was effective with six microsatellite loci, showing the extent to which subordinate foundresses lay eggs.

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**MONOANDRY AND POLYANDRY IN BUMBLE BEES
(HYMENOPTERA, BOMBINAE) AS EVIDENCED BY
HYPERVARIABLE MICROSATELLITES**

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Hypervariable microsatellites enabled a precise assessment of the number of queen matings in the colonies of five bumble bee species. Fifteen of the sixteen microsatellites initially cloned from *B. terrestris* had flanking regions similar enough to allow PCR amplification on the other *Bombus* species analyzed. The microsatellites selected for intra-colony study were characterized by a high heterozygosity (0.58-0.93) and a large number of alleles (3-18) in the local populations from which the colonies originated. A single male appeared to have inseminated the queens in the colonies of four species, *B. terrestris*, *B. lucorum*, *B. lapidarius* and *B. pratorum*, which belong to three subgenera. This suggests monoandry as a general feature in the genus *Bombus*. With one monoandrous and two polyandrous nests (minimum number of two and four patriline respectively), *B. hypnorum* represents a special case.

MULTILOCUS DNA-FINGERPRINTING IN ANTS

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Little is known about the mating frequencies of ant queens. We established a multilocus DNA-fingerprinting technique suitable to evaluate the number of patriline in singly-queened ant colonies. From individual *Camponotus*, *Pachycondyla*, and *Paltothyreus* workers we isolated between 5 and 15 μg of genomic DNA. The total amount of DNA was digested with restriction enzymes and hybridized with synthetic oligonucleotides after electrophoretic separation and blotting of the fragments. Radioactive and non-radioactive methods were used for detection of the hybridized probes. Combinations of 13 restrictionenzymes (so called "four cutters", e.g. Hae III, Hinf I, Cfo I) and five oligonucleotide probes (e.g., (CA)₈, (CAC)₅) were examined. In *Camponotus*, a combination of the restriction enzyme Hae III and the probes (GACA)₄ or (GATA)₄ gave the best results, i.e. clear banding patterns consisting of appr. 25 bands in the range between 4.0 kb and 23.1 kb with some interindividual variation. In the ponerines *Pachycondyla villosa* and *Paltothyreus tarsatus*, a combination of the restriction enzyme Sau 3A I and (GACA)₄ or (GATA)₄ yielded the best results, whereas Hae III with (GATA)₄ or (GACA)₄ gave less variable patterns. We calculated a simple band sharing index to get information on the average intercolonial variability of fingerprint patterns. The values for *C.floridanus*, *C. herculeanus* and *C.ligniperda* were 0.65, 0.5, and 0.6, respectively, those for *P. villosa* were 0.55. These values are rather high in comparison to non-social insects and vertebrates. Nevertheless, detectable variation was much higher than in allozyme studies. By comparing the banding patterns of the mother queen and her female progeny in single-queen-colonies it was possible to estimate the minimum number of matings. Our results show that in at least one of four tested colonies Of *C.floridanus* more than one patriline were present. Similarly, in colonies of *C.ligniperda* and *C.herculeanus* the queen was also multiple mated.

MICROSATELLITES FOR MEASURING RELATEDNESS IN *FORMICA* ANTS

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Estimating genetic relatedness among nestmates is important to assess the role of kin selection in the evolution of social behaviour. Relatedness can be estimated from allozymes datas, but fine scale measures are often limited by the low level of enzymatic polymorphism in social Hymenoptera. Microsatellites are DNA segments with short, tandemly repeated, nucleotide motifs. They are highly polymorphic because of variations in the number of repeats of the motif, and this length variability can be analyzed directly by electrophoresis of the polymerase chain reaction (PCR) products. The high number of alleles at microsatellite loci will permit a detailed analysis of colony and population genetic structure. Microsatellites were isolated and characterized in a highly polygynous red wood ant, *Formica lugubris*. A partial genomic library was screened with TG/AC and TC/AG oligonucleotidic probes, and 21 positive clones were isolated and sequenced. Primers were designed for PCR amplification of microsatellites, and several loci were surveyed in a local population. Two loci revealed 5 and 4 alleles in 22 workers taken from separate mounds (expected heterozygosity of 0.79 and 0.25, respectively). These primers were successfully used in other ant species of the genus *Formica*, and one locus proved to be highly variable in *Formica exsecta* (15 alleles in 27 individuals; expected heterozygosity 0.93). The primers did not permit to amplify microsatellites in species of other genera. I will discuss how microsatellites can be used to: 1) determine the number of matings, 2) measure genetic relatedness at different levels and 3) distinguish two sympatric cryptic species.

PHYLOGENETIC RELATIONSHIPS AMONG BEES INFERRED FROM NUCLEAR AND MITOCHONDRIAL DNA SEQUENCES

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Hypotheses about the evolutionary relationships among honey bees, including fossil and extant taxa, have been largely based on morphological or behavioral characters. Within the honey bee genus, *Apis*, uncertainties remain concerning the number of valid species throughout its range, including the center of diversity in Southeast Asia. Within *A. mellifera*, a species allopatric to its congeners, uncertainties remain concerning the genetic relationships of certain racial lineages among the 25 identified subspecies. Although honey bee subspecies are defined by morphological variation, DNA sequence variation can be used to provide additional characters for phylogenetic reconstruction. In this study we collected and analyzed sequence data from both mitochondrial and nuclear DNA regions to test phylogenetic hypotheses at the specific and subspecific level in honey bees. Oligonucleotide primers were developed to PCR-amplify a 700 bp region of the ND2 gene of the mitochondrial DNA and a 220 bp nuclear region containing an intron of the cytoplasmic elongation factor gene EF-1 α . Amplified products were cloned, DNA was purified from clones and both complementary strands were sequenced for multiple clones. DNA sequences were aligned and a matrix of informative characters were analyzed by PAUP. DNA sequence from the ND2 and EF-1 regions were informative at various taxonomic levels. We compare the concordance of our trees with previous hypotheses based on morphology, behavior and other molecular characters.

GEOGRAPHICAL POPULATION STRUCTURE IN THE PONERINE ANT *RHYTIDOPONERA* SP 12 (NR MAYRI) AS DETERMINED BY MITOCHONDRIAL DNA ANALYSIS

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Mitochondrial DNA (mtDNA) types from 74 nests of the polygynous arid-zone ant were analysed from single ants. Cytochrome b gene was amplified using polymerase chain reaction (PCR) technique, followed by analyses using restriction fragment-length polymorphism (RFLP), denaturing gradient gel electrophoresis (DGGE) and sequencing. Inter-colony analysis found that haplotypes are clumped, possibly due to the limited dispersal of wingless females, while intra-colony analysis found more than one haplotype in some colonies, suggested that colony founding involved unrelated gamergates. The results from DGGE, RFLP and sequencing will be compared, and their implications for the biology of this ant species discussed. Results from this study indicate that the analysis of mtDNA using PCR and DGGE techniques is well suited to population studies of organisms where small body sizes can sometimes be problematic.

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The analysis of relatedness and reproductive traits in the polygynous ant, *Leptothorax spinosior* Forel, using microsatellite DNA polymorphisms

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Leptothorax spinosior Forel lives on flood plains near rivers. About a half of the colonies have multiple queens (2-20) in our study field. In polygynous colonies, almost all queens were inseminated and laying eggs. No dominance behavior was observed among queens in a same colony.

Evaluation of relatedness among inter- and intracolony members should be useful for further understanding of polygyny. We designed primers from DNA sequences of *L. spinosior* to amplify (GT/AC)_n dinucleotide segments by polymerase chain reaction (PCR). Band patterns of PCR products shows that GT dinucleotide repeats are highly polymorphic in this ant. We detected interindividual microsatellite DNA polymorphisms and estimated the relatedness. The relatedness among queens from same colony was shown to be considerably high in *L. spinosior*.

We are also examining reproductive traits - the deviation of the reproduction among queens, determination of the allele of mated male and worker reproduction.

DNA FINGERPRINTING AND THE FORENSICS OF PARENT-OFFSPRING CONFLICT IN A EUSOCIAL BEE

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Demonstrating the importance of haplodiploidy in the evolution of eusociality requires estimation of four parameters: Relatedness between cooperating individuals, mating frequency, sex ratio, and rate of worker reproduction. Multilocus DNA fingerprints allowed precise estimation of these parameters for 12 eusocial (mother-daughter) and 12 parasocial (sister-sister) colonies of the primitively eusocial bee *Augochlorella striata* (Halictidae). Band-sharing proportions identified 8% unrelated workers. Genetic distinctness of these unrelated workers was due to multiple maternity, not multiple paternity. Because *A. striata* is monogynous, unrelated workers could be offspring of egg-dumping conspecific females. Mating frequency was uniformly monandrous. Consequently, workers in eusocial colonies were three times more related to female ($r=0.786\pm0.011$) than to male reproductives ($r=0.240\pm0.038$), following Reeve *et al.*'s band-sharing procedure. Diploid males due to sib-mating were found in one parasocial colony. Worker reproduction was evident only in parasocial, but not in eusocial colonies, and accounted for 9% of the males in parasocial colonies. Diploid males and worker reproduction confounded sex-ratio estimates of parasocial colonies. Even when correcting for worker reproduction and diploid males, sex ratios of parasocial colonies remained significantly more male-biased than sex ratios of eusocial colonies. Because of haplodiploidy, workers in eusocial colonies are more closely related to female than to male reproductives, while workers in parasocial colonies are equally related to female and male reproductives. The observed sex-ratio difference therefore suggests that workers facultatively adjust the sex ratio and, in eusocial colonies, capitalize on relatedness asymmetries by biasing the sex ratio toward closely related sisters. The present study therefore corroborates recent evidence for queen-worker conflict over the sex ratio, and implicates the role of haplodiploidy in the evolution of worker behavior in *A. striata*.

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CAUSAL FACTORS IN THE ORIGIN OF TERMITE EUSOCIALITY

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Chromosomal translocations and inbreeding patterns have been proposed as mechanisms which could create relatedness asymmetries promoting the evolution of altruistic sacrifice of reproduction by workers and from that the origin of termite sociality. However lower termite sociality is not founded on true worker caste sterility nor even on the sacrifice of reproductive value by pseudergates. Such explanations are therefore inappropriate for the Isoptera. Theorists have made much ado over the wrong questions. Relatedness asymmetries are not relevant. The retained ability of pseudergates to become alates and their universal ability to undergo neotenic sexual maturation indicate that pseudergate-based sociality presents no real evolutionary paradox in terms of lost reproductive value. The development of facultative neoteny in a proto-termite ancestor must have been a crucial enabling event in termite social evolution. The consequent reproductive plasticity would have promoted pseudergate origin by abolishing the reproductive cost associated with prolonged developmental stasis in late instars (stationary pseudergate moulting). Moreover, with the potential for nest inheritance, the pseudergate-neotenic developmental path would have enhanced reproductive value. The social behavioural repertoire of lower termite nymphs and pseudergates consists of low-cost acts--nest excavation, nest maintenance, and the feeding of parents and small nymphs. These behaviours require no special evolutionary explanations. In fact, lower termites exhibit considerable selfishness, engaging in manipulative biting of wing pads and legs (the proximate mechanisms of pseudergate determination) and siblicidal neotenic combat (exhibited most profoundly among the Kalotermitidae). The following factors provide a sufficient explanation of the origin of pseudergate-based termite eusociality: *excavatory endoxylophagy* and its implications on nutrition, cost of nest foundation, value of nest inheritance, generational overlap, potential for behavioural interaction, etc.; *facultative neoteny* and its consequences on developmental and reproductive plasticity; *manipulative biting* providing a proximate mechanism of pseudergate determination; and *monogamy* creating a relatedness parity among parents and offspring thus favouring ordinary forms of nepotistic and mutualistic beneficence among immediate kin. The origins of soldiers and true workers are secondary events and should be addressed as separate questions.

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EVOLUTION AND ONTOGENY OF TERMITE POLYETHISM

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It has been hypothesized that due to their hemimetabolous development, termites should have evolved an almost fully discretized caste system (Oster and Wilson, 1978), with each instar specializing on certain tasks. However, studies on division of labor of the dampwood termite Zootermopsis angusticollis show that there is an absence of age-related behavioral specialization both during the young (Rosengaus and Traniello, 1993) and older stages of colony development. There are probably ecological, physiological and developmental constraints in this, and other lower termite species, that override the evolution of specialized instars. Factors such as small colony size, low oviposition rates, simple nest architecture, lack of foraging, developmental flexibility (with stationary and/or regressive molts) and the potential for attaining reproductive status may have counteracted the evolution of task specialists. Higher termites, on the other hand, exhibit factors that may promote age-based division of labor and correspondingly, their caste organization seems to reflect a higher degree of age/task specialization paralleling the temporal polyethism exhibited by several complex hymenopteran societies.

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**POLYPHYLETIC ORIGINS OF THE SNAPPING
MANDIBLE AND ASYMMETRY, AND THE BIOGEOGRAPHY
OF SOME TERMITINAE (ISOPTERA: TERMITIDAE)**

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The Termitinae contains a number of genera related to *Termes* Linnaeus and *Capritermes* Wasmann, in which the mandibles of the soldiers are highly specialised and are not used for biting but as springs to strike enemies. Current interpretations of the relationships between those genera suggest that they are derived from an Ethiopian group of genera, related to *Cubitermes* Wasmann, with slender biting mandibles. The group is further divided into genera with symmetrical mandibles, and those with asymmetrical mandibles, the latter being derived monophyletically from the former. An examination of a number of characters, including imago-worker mandibular dentition, gut structure and soldier morphology, and considering geographical distribution, suggests that asymmetry is not monophyletic, and that the snapping mandible itself is diphyletic. The hypothesis also suggests that a stock with snapping mandibles, which gave rise to a group of relatively primitive genera related to *Termes*, was widely distributed in Gondwanaland before it fragmented into the present southern landmasses. A second large group of genera, related to *Procapritermes* Holmgren, is likely to be derived from a separate primitive stock which also gave rise to the *Cubitermes* group, and possibly the subfamily Apicotermitinae.

CLOSE EVOLUTIONARY HISTORY OF COCKROACHES AND TERMITES AS DEDUCED FROM PRIMARY STRUCTURES OF AKH-PEPTIDES

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Small peptides with adipokinetic and/or hypertrehalosaemic activities have been isolated and sequenced from corpora cardiaca of insects from all major orders including the Dictyoptera of which only mantids and cockroaches were analysed until now. Here we report on isolation and identification of such peptides from termites. Throughout purification we used the locust adipokinetic bioassay to monitor activity. Isolation was achieved from head extracts of *Microhodotermes viator* (Hodotermitidae) and *Trinervitermes trinervoides* (Termitidae). Structure elucidation by Edman sequencing and mass spectrometry revealed the sequences shown below. Comparison with the peptides from cockroaches and mantids result in the following interpretation:

The peptide from the Termitidae is identical to a peptide found in blattid cockroaches (pGlu-Val-Asn-Phe-Ser-Pro-Asn-Trp-NH₂) and very likely to that in Mastotermitidae as well, whereas the peptide from Hodotermitidae (pGlu-Ile-Asn-Phe-Thr-Pro-Asn-Trp-NH₂) is similar, but not identical to either a peptide in a polyphagid cockroach (pGlu-Ile-Thr-Phe-Thr-Pro-Asn-Trp-NH₂) or to one in various mantids (pGlu-Val-Asn-Phe-Thr-Pro-Ser-Trp-NH₂). Based on these data, termites could be viewed as a sister group to both, cockroaches and mantids, supporting recent findings based on morphological and behavioural characters.

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A COMPARISON ON SOCIALITY BETWEEN TWO XYLOPHAGOUS
COCKROACHES, PANESTHIIDAE AND CRYPTOCERCIDAE

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In discussion on the evolution of eusocial organization in Isoptera (termite), the Blattaria (cockroach) is of special interest among the non-eusocial insects. Because both insects are believed to be very closely related phylogenetically. Among the 4000 species of cockroaches in the world, three species of Cryptocercidae and over one hundred species of Panesthiidae are known to be wood-feeding and wood-dwelling cockroaches. In evolutionary terms Panesthiidae is considered to be more advanced than Cryptocercidae. However, the life styles of many species in Panesthiidae are very similar to Cryptocercidae. For example, the colony compositions of Salganea spp. and Macropanesthia are known as subsocial that these cockroaches are living in a family group. In this study, I compared my findings on social behavior of Salganea and Macropanesthia with published account of the social behavior of the other panesthine species and Cryptocercus punctulatus. The similarities in their social behavior and external morphologies between some genus of Panesthiidae and Cryptocercida are considered to be an example of convergent evolution.

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**MALE REPRODUCTIVE INVESTMENT IN PAIRS OF
THE WOOD ROACH *CRYPTOCERCUS PUNCTULATUS***

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Adults of the wood roach *Cryptocercus punctulatus* form monogamous pairs, overwinter together, then produce their sole set of offspring nearly one year after the initial pairing. Field and laboratory evidence suggests that copulation occurs repeatedly over the course of the association. Males and females mate shortly after pairing, but also prior to, during and after their reproductive period; spermatophores have been found in females as much as one year after offspring production. Studies were conducted to determine the effect of 1) a resident male and 2) multiple mating on the production and development of offspring. During autumn of 1991 and 1992, recently paired adults were collected from the field and treated in one of the following ways: (A) The male was removed. (B) The male was surgically rendered unable to copulate. (C) The tarsal segments of the male's right metathoracic leg were removed (surgical control). D) Virgin adult females were paired with virgin males that had been surgically altered as in (B) (technique control). Treatments were placed into field boxes and left undisturbed until fall (October-November) of the following year. Boxes were then opened, survival and reproduction noted, and offspring counted and measured. Pairs that survived without reproducing were replaced in the field and checked during the second autumn following treatment. The results suggest that the presence of the male influences female reproduction; mated females can produce offspring if a male is not present, but they are less likely to do so. Sperm are viable in the spermatheca for at least two years. Among females that reproduced, neither the male's physical presence nor his ability to mate had an influence on the number or early development of offspring.

**CRYPTOCERCUS AND THE ORIGIN OF EUSOCIALITY
IN TERMITES: A PHYLOGENETIC APPROACH.**

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The three species of *Cryptocercus* cockroaches are xylophagous and harbour flagellates, and *Cryptocercus punctulatus* at least is familial. This species is classically mentioned as documenting a particular evolutionary route, namely a subsocial origin for the eusociality of termites. Considering that the correct context for macroevolutionary studies is the monophyletic lineage including the taxa under study, I developed (in collaboration with P. Grandcolas) a phylogenetic approach to this question. Phylogenetic analysis allows to test evolutionary hypotheses through the test of scenarios. For reasons of weakness of a priori similarity criteria, behavioural and ecological traits were not used as phylogenetic characters in the analysis, but instead were treated as "attributes", the history of which being traced relatively to a phylogeny based on other traits. The phylogeny of cockroaches was revised on morpho-anatomical grounds, and 17 different informative characters make *Cryptocercus* a member of the cockroach subfamily Polyphaginae, belonging to a group including *Therea*, *Ergaula* and *Eucorydia*. The distribution of attributes (familial habits and xylophagy) on this phylogeny supports by far one most parcimonious evolutionary scenario, namely that the socio-ecological traits of *Cryptocercus* evolved independently in the lineage Polyphaginae, and have no common history with the analogous characteristics of eusocial termites (apart from remote inheritance of poorly specific traits like heterometaboly). This perspective could be changed only on the basis of a (possible) further revision of the phylogeny, based on more characters or improved character analysis and phylogenetic methods. Thus, the history of the origin of eusociality in termites is presently completely undocumented, and the convergent characteristics of *Cryptocercus* cannot be invoked to fill the gap. The misleading notion of *Cryptocercus* being a "primitive cockroach" has no biological support, and it impeded the understanding of evolution in this lineage. On the other hand, we can now develop the study of the evolution of familial habits in *Cryptocercus* in the identified correct phylogenetic context: the cockroach monophyletic lineage Polyphaginae.

WHEN DID *CRYPTOCERCUS* COCKROACHES GET THEIR PROTOZOA SYMBIONTS FROM TERMITES?

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The cockroach *Cryptocercus* harbours as some Termites a fauna of Protozoa symbionts. The recent revision of its phylogenetic position among cockroaches showed that it actually belongs to the subfamily Polyphaginae (Grandcolas & Deleporte, 1992; Grandcolas, 1994). It implies that its symbiotic Protozoan fauna has been acquired by transfer from Termites. An hypothesis of transfer was already proposed but without clear phylogenetic arguments and was assumed to be very ancient, following the current opinion about *Cryptocercus* antiquity (summarized by Thorne, 1990). The phylogeny of Polyphaginae is used to carry out a parsimonious biogeographical analysis to date the Protozoa transfer. *Cryptocercus* has an amphi-Beringian distribution (East Asia and North America), while its closest relatives are distributed in India (*Therea*), South Asia (*Eucorydia*), South East Asia and Africa (*Ergaula*). A phylogenetic scenario concerning these distributions implies that the ancestor of *Cryptocercus* was distributed only in Asia, extending posteriorly its distribution to North America. A significative event is the vicariance [India vs East Asia] between *Cryptocercus* and *Therea*: it may have taken place not before Miocene when India came near Eurasia and when Tethys sea was closed (Scotese et al., 1988). The subsequent extension of the *Cryptocercus* distribution to Eastern and Western North America was possible up to the Pliocene (with Bering Strait and holartic mesothermal broad-leaved or microthermal coniferous forests) (Wolfe, 1985). This date is recent (23 Millions of years) and has no common measure with the those previously proposed, even by the followers of the transfer hypothesis (Thorne, 1990).

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PHEROMONES AND PHEROMONE PRODUCING GLANDS IN COCKROACHES AND TERMITES: COMPARAISON AND THEIR EVOLUTIONARY SIGNIFICANCE.

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Cockroach and termite pheromones have been extensively studied but only seven were identified in cockroaches, a group with about 4000 living species, and two among the 2000 living species of termites. These nine pheromones are chemically completely different, only two belongs to the same chemical class, the 4,6,8-trimethyl-7,9-undecadien-5-ol, a female specific compound present in the tergal glands of *Cryptocercus punctulatus* and the (3Z,6Z,8E)-3,6,8-dodecatrien-1-ol, which is secreted by the sternal glands and act both as a sex and as a trail pheromone in the termite *Pseudacanthotermes spiniger*. In termites workers, the trail pheromone is produced by the sternal glands, a gland which produce the sex pheromone in virgin females. In most of the cockroach species, the male or female sex pheromones are produced by tergal or sternal glands. In adults of *Blatta orientalis* we found that on the same tergite, gland cells on the anterior part produce the male sex pheromone while those on the posterior part produce aphrodisiacs. In adult females, as in the larvae of both sexes, a defensive glue is secreted by the tergal glands. All these glands have the same morphology with the same kind of gland cells. In *C. punctulatus* and in termites where the secretions consist mainly of one major compound, the very complex organization of the pheromone producing glands indicates a great similarity in the fine structure.

The existence of an ancestor common to cockroaches and termites remains the most logical explanation for the observed similarities. Until now the discussion focused on *Cryptocercus* and lower termites. The study of the exocrine glandular system and its secretions in several poorly known cockroaches sub-families would contribute to a better understanding of the pheromonal communication in these two groups.

PRIMITIVE ANTS

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Unlike the other eusocial Hymenoptera, ants are all highly eusocial and lack closely related species that display a solitary lifestyle. Consequently the search for an understanding of the evolution of social behavior in ants has focused on taxa within the Formicidae that are regarded as primitive by virtue of their possession of less derived morphological characters or by the absence of behavioral characteristics that are thought to be more derived. In this symposium we have brought together investigators who are studying a diversity of aspects of the biology of ants in the three subfamilies that are usually regarded as being primitive: the Myrmeciinae, the Nothomyrmecinae, and the Ponerinae. Of these, the first two are restricted in distribution to Australia, while the ponerines have a worldwide distribution, with their greatest diversity in the tropics. The extensive adaptive radiation of the ponerines brings into question whether all members of this subfamily are, indeed, "primitive", and as various authors in the symposium point out, drawing evolutionary conclusions concerning social behavior based on clades rooted in the ponerines can be tricky. There can be no doubt, however, that the questions raised about the social behavior of these subfamilies is interesting and that the studies in this symposium provide information that helps us to understand ant evolution and adaptation.

**THE SOCIOBIOLOGY OF *NOTHOMYRMECIA MACROPS*:
CONSIDERATIONS REGARDING THE EVOLUTION OF
EUSOCIALITY AMONG THE ANTS.**

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Field experiments and observational studies on *Nothomyrmecia* will be summarised, with special reference to social organisation and the behaviour of individual larvae, workers and queens. Topics will include: evidence for the almost total lack of polyethism in this «least sociable of eusocial insects» ; colony foundation ; relations between workers, workers and brood, and workers and queens ; foraging and feeding behaviour ; diurnal patterns of foraging activity and navigation.

The levels of sociality in *Nothomyrmecia* and other ants, including *Myrmecia* and *Amblyopone*, will be compared, and relevant similarities and differences reviewed. Shared characteristics include the relatively great longevity of workers and queens, queen allectomy after mating, aspects of colony foundation, the presence of a metapleural gland, retention of the brood in a single chamber, not in separate cells, burial of larvae for cocoon spinning, etc. The adaptiveness and evolutionary acquisition of these attributes will be discussed, and the possible characteristics of the last non-eusocial ant ancestors considered, with the suggestion that there might have been several alternative paths of evolution from pre-eusocial to eusocial formicids.

EFFECTS OF AGE ON BEHAVIORAL PROFILE IN THE
PRIMITIVE ANT *AMBLYOPONE SILVESTRII*

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Behavioral differentiation (division of labor or polyethism) related to age-size difference in the worker caste has been well documented in several species of ants (Hölldobler and Wilson 1990 for review). Recently, the study of polyethism has also been extended to some ponerines (e.g. Corbara et al. 1989) and *Nothomyrmecia* (Jaisson et al. 1992), whether or not referring to age. However, information on this aspect in the primitive genus *Amblyopone* has been much limited, excepting for *Amblyopone pallipes* (Traniello 1978). In *A. pallipes*, social behavior of worker ants showed no fidelity to their age and thus this species has been considered lacking age polyethism. I have studied division of labor and its relationships to age and body size in two mature colonies of *Amblyopone silvestrii*. Data from each colony were analyzed with multivariate analyses (principal component analysis and cluster analysis). The results clearly showed that division of labor in workers of *A. silvestrii* was based on their age. The pattern of this age polyethism is essentially the same as generally known in advanced species of ants and social bees: older individuals perform most foraging while younger individuals are more active in brood care. In addition to workers, natural nests of *A. silvestrii* often contain a small number of dealate but uninseminated females. Laboratory observation suggested that these females are individuals remaining in nests where they were born. Their smaller body size, in comparison with queens (=fertile inseminated females), would have resulted in a smaller possibility of successful colony founding and may account for their remaining sterile and functioning as workers in their natal nest.

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DIVISION OF LABOUR IN THE ABSENCE OF THE ERGATOID QUEEN IN *PLECTROCTENA MANDIBULARIS* (HYMENOPTERA: FORMICIDAE: PONERINAE)

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Division of labour was studied in three ergatoid-less colonies of the ponerine ant *Plectroctena mandibularis*. Self-oriented acts (including self-grooming, inactivity in and outside the nest, walking in and outside the nest, and feeding) constituted more than 70% of the social ethogram in all colonies. Brood-related activities were absent as no workers laid eggs, while the frequencies of social interactions between workers were low (less than 2%) revealing a tendency by the workers not to engage in social contact. Agonistic interactions between workers occurred only in the early part of the study and it is possible that one or more dominance hierarchies were established in the colonies. This is further supported by the formation of worker "factions" where groups of workers were spatially separated from each other. Effect of the absence of the ergatoid on division of labour was quantified by assessing the increase in inter-cluster distances (ICDs) between groups of workers revealed by hierarchical cluster analysis. Inter-cluster distances of 0.7 have in the past been adequate for delimiting meaningfully homogenous groups of workers with similar roles. In all three colonies at an ICD of 0.7 each individual was identified as a single group, while groups of workers (where behaviours best characterizing groups are not self-oriented) are recognized only at ICDs of 1.4 and above. This fragmentation of the division of labour is attributed to the absence of the ergatoid queen, whereby the workers are released from pheromonal suppression of the ovaries. These pheromones, therefore have an additional (and indirect) function in that they maintain colony structure, integrity and productivity.

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ONTOGENY OF SOCIAL BEHAVIOUR AND NESTMATE BROOD RECOGNITION IN A PONERINE ANT

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Nestmate brood recognition has been little studied in Ponerine ants and results seem contradictory (cf. Crosland, 1988; Jaisson et al., 1992). Our first report on *Ectatomma tuberculatum* Ol. has demonstrated that groups of workers are able to discriminate nestmate from non-nestmate conspecific brood. However only nurses show a clear preference for nestmate larvae and pupae (Fénéron and Jaisson, 1992). The present study analyses the development of nestmate brood discrimination capacity and its relation to social status. As it is known in other species, *E. tuberculatum* workers perform successively distinct behavioural stages: inactivity, brood care, colony maintenance, guarding the nest entrance and, finally, foraging. During this behavioural ontogeny, it appears that only 2-to-10 week old adults (nurses) prefer nestmate larvae. Younger as well as older workers are unable to discriminate brood. Further experiments, using intraspecific adoptions, reveal that the development of recognition capacity depends on the social status of the worker and on its spatial proximity to the brood, rather than a strict age-related maturation. They demonstrate also that callow workers learn to recognise and prefer nestmate brood, even when it is unrelated. The fact that workers usually stay inside the brood chamber during the first few days of their life may facilitate learning.

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THE SEARCH FOR FOOD: THE TRANSITION FROM SOLITARY TO SOCIAL FORAGING IN A PONERINE ANT, *PARAPONERA CLAVATA*

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Paraponera clavata workers forage solitarily for nectar and insect prey, but can facultatively engage other workers in social foraging by recruiting those workers to a food resource. The purpose of these experiments was to investigate the factors that govern the shift from solitary to social foraging and to place the foraging strategy of *P. clavata* into an evolutionary context. The foraging behavior of *P. clavata* was investigated at the La Selva Biological Station in Costa Rica. Ants produce individually discriminable odor trails (Breed and Harrison, 1988) which can be used as guidelines for the forager or as recruitment trails (Breed et al. 1987). The probability of recruitment occurring is sensitive to the type of food discovered, the quantity of food, and the distance of the food from the colony. Search strategies vary among individual ants, and an ant tends to display constancy in its search pattern. The foraging system of *P. clavata* resembles that of other ectatommine ants, such as *Ectatomma* (Breed et al., 1990) and differs substantially from the patterns reported for other ponerine ants. *P. clavata* displays nearly all of the foraging communication mechanisms of mass-foraging myrmecines, such as *Solenopsis*, but exhibits a transitional mode between complete reliance on individual foraging and a complete reliance on mass foraging.

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The army ant behaviour and recruitment of the ponerine ant *Simopelta* sp. with very small colony size

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Simopelta is one genus of Ponerinae and is distributed in the tropics of New World. The species of this genus prey on pupae and larvae of other ant species, especially *Pheidole* sp., by group raid. Although they have been regarded as army ant by a few simple observations (Wilson 1958, Gotwald 1966), the detailed habit of *Simopelta* is unknown yet. In Barro Colorado Island (BCI) of Panama, Central America, we collected 27 colonies of *Simopelta* sp. 1 which is undescribed yet. On the basis of two behavioural characteristics of army ant: group foraging and frequent colony emigration, the legionary habit of this species was investigated.

On the tropical rainforest floor, the *Simopelta* sp. 1 colonies nested in the hole of fallen branch and twig which *Pheidole* sp. or other ant species often inhabited as well. Their colony size was very small ($24.2 \pm \text{SD}15.0$). In observation of laboratory, the workers of *Simopelta* sp. 1 exhibited group foraging with a persistent trail system. The size of foraging column was as small as 2.3 ± 0.6 workers on average. When workers encountered too large and too many prey such as centipedes and *Pheidole* sp. colony, they summoned any nestmates with special recruitment behaviour. The scout workers stimulated their nestmates with the chemical trail pheromone and the behaviour of running in the nest and guided them to the target prey.

In 13 colonies cultured for about one month, the colony emigration irregularly occurred 3.1 ± 2.2 times on the average. All members of colony were stimulated to emigrate by a scout worker like the recruitment behaviour for hunting. However, the nestmates can often trace the trail and arrive in the new nestsite without the guidance of the scout worker.

During colony emigration, the number of scouted workers in one recruitment was more than during hunting. Probably the scout workers may control the members with the time of running behaviour. This system appears to be the adaptation for frequent and rapid colony emigration.

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« BROOD MANAGEMENT » DURING COLONY
FOUNDATION OF *PACHYCONDYLA*
(HYMENOPTERA FORMICIDAE PONERINAE). *APICALIS*.

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Pachycondyla apicalis is a neotropical ponerine ant which lives in monogynous colonies. After mating and haplometrotic colony foundation, the new queens need to forage outside of the nest. The colony founding mode is a very interesting aspect of reproductive strategy in ponerine species because during the founding stage, queens have to achieve a balance between rearing brood and minimizing the frequency of foraging trips.

The demographic growth (brood and adults) of twenty founding colonies was studied in the laboratory. Only seven of these were able to produce a first worker (ergonomic stage) and only one survived to the reproductive stage after 20 months.

Before emergence of first worker, the queen has to care for three categories of brood and simultaneously leave the nest to search for food. Then she devotes all of her energies to rear the most advanced brood (larvae and pupae) in order to accelerate the emergence of the workers. We observed the periodic and massive disappearance of up 95 % of the eggs laid and 75 % of first instar larvae. Sacrificed brood is used to feed queen and larvae, particularly the oldest. The use of reproductive eggs as a food reserve may be an adaptive strategy enabling the foundress to minimize the number of foraging trips because a high risk of mortality is generally linked to the foraging activity of workers. However, in order to ensure the success of the colony, brood management implies the sacrifice of the most recently laid eggs. Consequently the flux of workers is not continuous, but an incipient colony produces age cohorts of callow workers which become more and more numerous. When the number of foraging workers increases, egg cannibalism is then reduced.

This brood management strategy may be frequent in ponerine ants that exhibit partially claustral mode of foundation. This system is a possible compromise between queen survival and colony rearing success.

DOMINANCE BEHAVIOR AND TROPHALLAXIS IN THE
PALAEARCTIC ANT *PONERA COARCTATA*

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Ponera coarctata is a small, cryptic, predatory ant occurring from Southern Spain over South England to the Black Sea. Its colonies can be found in the soil and contain approximately 30 to 60 rarely more than 100 workers. Some colonies possess two or three fertile queens, but most are monogynous. In the presence of reproductive queens, aggression among workers does not occur. However, only a few hours after queen removal workers begin to antennate each other aggressively. We also observed biting of the opponent's mandibles or antennae, which occasionally resulted in chasing the subordinate worker with widely opened mandibles through the colony. Agonistic encounters resulted in a dominance hierarchy, which appeared to be stable from the very beginning of dominance interactions. Dissections of the workers revealed differences in their ovarian development, which were correlated with their hierarchy rank. Workers do not possess a spermatheca but can produce viable eggs and rear male offspring in queenless colonies. Behaviors very similar to dominance interactions were observed in two other contexts, i.e. recruitment and trophallaxis. The interaction began in a similar way in all three cases: two ants approached and antennated each other, one ant started to open her mandibles and to bite the mandibles of her opponent. This either escalated into biting the antennae or other body parts, or the active ant pulled the opponent backwards, stopped, turned around and began to lead a tandem run. In the third outcome, both ants opened their mandibles, came into contact with their inner mouthparts and engaged in trophallaxis. Regurgitation in *P. coarctata*, however, is not connected with higher morphological specializations, such as a special crop morphology. Trophallaxis and recruitment behavior occur also in queenright colonies, but only queen removal reveals the close relationship between aggression, recruitment, and trophallaxis.

HOMOSPECIFIC KIDNAPPING IN A PONERINE ANT: *ECTATOMMA RUIDUM* ROGER (HYMENOPTERA, FORMICIDAE)

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Laboratory studies on interindividual interactions between homospecific colonies of the neotropical ponerine ant *Ectatomma ruidum* Roger, confirm for this species the very low level of homospecific aggression (Corbara, 1991) and the existence of cleptobiosis, or food robbing, as a facultative foraging strategy (Breed et al., 1990; Perfecto and Vandermeer, 1993). A new phenomenon was also demonstrated: the kidnapping of callow workers and brood (pupae and larvae) by workers belonging to two other colonies in which brood development had nearly stopped. These kidnappings show two original traits when compared with similar behaviors reported for other ant species: 1) Raids were made without any recruitment by individual thief ants apparently specialized in this kind of behavior. As was the case for cleptobiosis (Breed et al., 1992), it looks likely that these individual workers acquired the chemical camouflage of a given target colony in which they can stay for various hours, and specialized on raiding only that colony. 2) The target colony was a more developed, healthy one, colony than the one making the kidnappings. Callow workers kidnapped were all 0- to 3-days old: they were immediately integrated within the raiding colony and participated efficiently in brood care activities. Brood development was restored and larvae were reared to maturity: various worker eclosions were thus obtained in the raiding colonies. According to their characteristic patterns, we considered these kidnappings to be real intraspecific slave raids derived from cleptobiosis, which constitutes the first report of dulosis in the Ponerinae subfamily. The mechanism of these intraspecific, intercolonial slave raids constitutes an original model allowing the reconstitution of a primitive evolutionary precursor in the dulosis route leading to slavery in the more evolved subfamily Formicinae.

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FIRE ANT THERMOREGULATION

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Temperature is a central factor in the life of ant colonies. Colonies experience substantial changes in temperature from season to season, from day to day and even from minute to minute. Because temperature controls colony metabolism, some ants have become very effective thermoregulators.

This paper will focus on two key points of fire ant (*Solenopsis invicta*) thermoregulatory behavior: 1) mound building and 2) temperature tracking. In order to study the thermal benefits of mounds, I measured mound and soil temperatures at four depths (2, 15, 40, and 90 cm) for a year. At 2 cm, mounds averaged 7 °C warmer than the surrounding soil, at 15 cm the difference was 2-3 °C, and at 40 cm the difference essentially disappeared. The importance of the sun in heating the mound was demonstrated by the fact that mounds only provided a thermal benefit on sunny days. On cloudy days, mounds were almost the same temperature as the surrounding soil.

Fire ants regulate colony temperature by cycling up and down in their mound as it warms or cools. In order to study temperature tracking behavior, two colonies were excavated every other week for a year, one in the early morning and the other around midday. The distribution of workers and brood in mounds changed seasonally. Generally, brood were placed in the mounds whenever temperatures were higher than the surrounding soil but less than 35°C. Laboratory studies showed that well-fed colonies consistently preferred brood temperatures of 30-32 °C.

Fire ants clearly invest considerable time and energy in regulating colony temperatures, but how much does this behavior actually benefit colony growth? This question can be addressed by modelling the accumulation of developmental degree-days under different behavioral alternatives. The value of temperature tracking behavior was modeled in hypothetical colonies that tracked temperature changes and those that remained fixed at either 2 cm or 40 cm in the soil column. The results of this model indicated that tracking behavior provides a 13% yearly benefit over remaining stationary at 2 cm and about a 30% yearly benefit over remaining stationary at 40 cm.

The value of building a mound was evaluated by comparing the accumulation of degree-days for colonies living in the soil and colonies living in a mound. Both types of colonies were assumed to track changing temperatures. The thermal benefit of mounds was approximately 10% per year. This seems rather small, but mounds only provided thermal benefits on sunny days when temperatures were within the growth window. Most of the thermal benefit of mounds occurred in the spring and the fall when they warmed into the growth range but the surrounding soil remained too cold for brood development.

Temperature tracking behavior and mound building behavior, taken together, provided approximately a 23% thermal benefit compared to a hypothetical colony that did not thermoregulate but remained stationary in the soil.

TERRITORY SIZE AND SHAPE IN CROWDED POPULATIONS
OF THE FIRE ANT *SOLENOPSIS INVICTA*

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Traditional models of optimal territory size consider the decisions of single territory residents and assume implicitly that territories are not contiguous. However, in crowded conditions, the size of any particular territory depends not only on the actions of the resident, but also on the reactions of each of its neighbors, which unfold through a series of behavioral exchanges. An approach to modelling territory size in networks of interacting residents is described. The model is tested with the monogyne form of *S. invicta*; however, it can also be applied to other social insects or to animals in which territories are defended by individuals. It is assumed that each colony exerts pressure against its neighbors, as a result of its aggressive behaviors, and that boundaries are formed along lines at which the pressure applied by adjacent colonies is equal. The pressure at a particular point is a function of the size of the colony (the number or biomass of workers), the distance from the nest, and the current compression of the territory caused by competition. An iterative procedure is used to find the location and shape of each boundary given the positions and sizes of colonies. To test the model, territories of the monogyne form of *Solenopsis invicta* were mapped in pasture in north Florida, a habitat covered almost completely by exclusive foraging territories. Parameter values were estimated by fitting the model to a mapped mosaic. The significance of the fit was then tested with an independent data set from the same habitat. Predicted and observed territories were significantly correlated in size, in shape (length/width ratios), and in the distance and direction between the nest-site and the geometric center of the territory. The strengths of the correlations were greater than for methods that ignore neighborhood interactions. The basic framework can be modified to incorporate various assumptions about the mechanisms of fighting and assessment, the value of defended space, adaptive decision-making, colony migration, and biological details of particular species. However, even with very simple assumptions, the model successfully accounts for much of the variation in the sizes and shapes of territories mapped in the field. These results show that territories are molded by a balance of aggressive behavior among neighbors and that the outcome of interactions at one location depend upon events occurring elsewhere in the mosaic.

LABOR-SECTORS IN FIRE ANT COLONIES: ECOLOGICAL AND ONTOGENETIC FORCE?

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Using the fire ant, *Solenopsis invicta*, I considered the colony-level effects of aggregating the labor life-histories of workers during colony growth and development (sociogenesis) from founding to maturity. Mean worker weight, size-variability and longevity increase several-fold. The mean days in brood care, reserve and forager status changes with worker size. While somewhat flexible, labor-flexibility is limited by decreased efficiency when tasks are carried out by workers other than those normally doing so. I define the colony-sum of the total labor of a particular type as a *sector*. I estimated these sectors for fire ant colonies by multiplying the number of workers by the mean days at each type of labor. Total labor and the foraging sector grow more rapidly than does the colony, while the nursing and defense sectors grow more slowly, changing their proportions. These changes in sectors act as an ontogenetic feedback system, driving the sociogenic increase in worker size and fattiness through the changing proportions of the foraging and nursing sectors. They also act as an ecological force, affecting the outcome of the territorial competition with neighbors, and therefore population-level attributes. Ultimately, sectors must also affect the allocation of resources to reproductives, and therefore colony fitness. The sectors and their shifts are programmed into the life-histories of individual workers and are an emergent property of their colony-level summation. By acting on the rules of individual development, evolution may result in changes in the attributes of colonies. Sectors can be seen as the colony analogs of organs. They link individual-level phenomena with colony-level and ecological-level phenomena.

FORAGING IN LEAF-CUTTING ANTS: ENERGY
EXPENDITURE DURING CUTTING DETERMINES LOAD-SIZE
SELECTION.

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It has been repeatedly observed that foraging social insects often return from non-depleting food sources with partial loads. Although two different hypothesis have recently been advanced to explain the adaptive value of this observation, the proximate mechanisms underlying such behavior remain poorly investigated. Here we report evidence demonstrating that workers of the leaf-cutting ant Atta cephalotes adjust the size of the leaf fragment being cut to their metabolic expenditure while cutting. In laboratory experiments, ants were allowed to cut leaf fragments at two different temperatures, 25° and 40°C. Using measurements of cutting speed at both temperatures and previously published data on the increase of metabolic rate with rising temperature, we predicted what fragment sizes should be cut at 40°C if ants invest the same amount of energy as they invest during their cutting activity at 25°C. We then compared the predicted load-sizes with the sizes actually cut by the ants during the experiments at 40°C. Results indicate that foraging leaf-cutting ants start cutting a leaf fragment with a fixed amount of energy to be invested during the cutting activity. The more energy spent per unit time during cutting, the smaller the fragments selected by the foragers. A similar conclusion could be drawn after direct measurements of force produced by the worker's mandibles during cutting. Even though workers cut smaller fragments when foraging on tough leaves, total force developed to cut a fragment was similar for leaves of different toughness.

HOW COLONY AGE/SIZE AFFECTS COMPETITION FOR FORAGING SPACE AND POPULATION SPATIAL DISTRIBUTIONS

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A population of about 250 individually-identified colonies of the seed-eating ant, *Pogonomyrmex barbatus*, has been tracked for 12 years. Colonies are founded by a single queen, and reach a stable size of about 12,000 workers when the colony is about 5 years old. Young, growing colonies, about 3-4 years old, are more persistent and aggressive in conflict over foraging area than their older, larger neighbors of stable size. Foraging area may have prospective value for a young colony if it can acquire a foraging range to be used in the future, especially if some sites consistently provide valuable seeds. A study of seeds collected by ants showed no relation between seeds collected and local vegetation; most seeds collected by ants are widely dispersed by wind and rain. Foraging trails do not lead to distinct patches of particular seed species. Thus colonies are competing merely for space in which to search for seeds. A second line of evidence against the prospective value hypothesis is that a colony's foraging range one year only overlaps about half its foraging range of the previous year, so a young colony is not acquiring a foraging range to be held for the rest of its life. Surprisingly, a colony's foraging range does not increase linearly with colony growth: by the time a colony reaches the age of 2 years, with about 2,000 ants, its foraging range is as large as that of a 5-year-old colony with 12,000 ants. However, the small, young colony does not cover all areas of its foraging range as frequently as larger ones; this is confirmed by a study of the effects of colony age/size, and the density of nearby colonies, on the rate and outcome of repeated encounters between neighbors. A 3-4 year old colony may be just large enough to afford to defend its newly-acquired foraging range; an older one may avoid conflict because this is when they begin to produce sexuals. At the population level, spatial distribution of colonies show that age-dependent changes in foraging and territorial behavior influence the spatial distribution of colonies.

ROLE OF HOST ANT BEHAVIOR IN THE EVOLUTION OF EXTREME HOST SPECIFICITY IN PHORID PARASITOIDS (DIPTERA: PHORIDAE)

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Phorid parasitoids of foraging adult ants are typically very host specific. I propose that the evolution of this extreme host specificity is the result of two features of ant behavior. First, individual foraging ants are protected from parasitoid oviposition by their hard exoskeleton, agility, structural weapons (mandibles and stings) and specialized defensive postures. Moreover, colonies have evolved specialized social defenses that further reduce access to susceptible workers. To successfully counter host defense mechanisms parasitoids require a structurally specialized ovipositor and careful, specialized approach behavior. Second, host specificity may be enforced still further through the cues parasitoids use to find hosts. Some of the most reliable cues available to these parasitoids are the pheromones ants use to recruit nestmates to newly discovered food sources (recruitment pheromones) or to direct colony defense against enemies (alarm pheromones). To the extent that these pheromones are species-specific, they may control the degree of host specificity of parasitoids and thereby affect the probability of coevolution among hosts and parasites. Recruitment pheromones are diverse with a high degree of species specificity, whereas alarm pheromones are less diverse and tend to evolve convergently in different ant lineages. The phorid parasitoid *Apocephalus paraponerae* uses two products from the mandibular glands of its primary host (*Paraponera clavata*) as cues to locate ants for oviposition. These compounds (4-methyl-3-heptanone and 4-methyl-3-heptanol) act as alarm pheromones in several species of ponerine ants and the pattern of host use by *A. paraponerae* is coincident with the distribution of these compounds. Species in other lineages of *Apocephalus* are more host specific than *A. paraponerae*, and circumstantial evidence supports the use of recruitment pheromones as location cues in these lineages. These patterns suggest that use of alarm pheromones as host location cues may offer greater opportunity for colonization of novel hosts than does the use of recruitment pheromones. This leads to the prediction that lineages of phorid parasitoids that use alarm pheromones as host location cues should be less host specific and show less extensive cospeciation with their hosts than lineages that use recruitment pheromones. A definitive test of this hypothesis requires information on the phylogenetic relationships of both hosts and parasitoids, as well as information on the distribution of chemical substances used as pheromones and host location cues.

MATING BEHAVIOR OF THE POLYGYNOUS WOOD ANT - *FORMICA AQUILONIA*

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The diversity of mating systems found among ants can be grouped into two major syndromes, "female calling" and "male aggregation" (Hölldobler & Bartz 1985). The relatively few studies of mating behavior in the genus *Formica* indicate that elements of both syndromes are present within single *Formica* species. I study the mating behaviour of the highly polygynous *Formica aquilonia*, in laboratory conditions. Based on video recordings I separate the mating process into three phases, a) initial phase (from first physical contact to genital contact), b) still phase (from establishment of genital contact to first movement of either sex) and c) terminal phase (from the end of the still phase until the genital contact is broken). I demonstrate multiple mating for both sexes and female mating numbers are found to be in good agreement with results for the effective number of matings based on allozyme mother-offspring analyses (Pamilo 1993). In random associations of males and females mate choice seems to occur at random. In choice experiments I detect no difference between the frequencies of intra- and intercolony matings. Neither does the mating status of males or females, nor the operational sex ratio in the experimental chamber, affect the pattern of random matings. However, the number of preceding matings for both sexes affects the duration of different parts of the mating process. Thus, female mating resistance is higher after several matings, and the duration of genital contact increases with the number of preceding male matings. Also, male mating experience reduces the time used to get into genital contact, but a high frequency of matings contradicts this effect probably because of male exhaustion. I discuss sexual selection present in *F. aquilonia* with special reference to the occurrence of polyandry. I concentrate on individual-level selection since most colony-level hypotheses are based on polyandry increasing genotypic diversity, and are thus not likely to be applicable to highly polygynous colonies. The disability of ant males to produce more sperm after maturation may generate selection for male mating behaviors based not on a maximal, but on an optimal number of matings. Thus, the multiple mating of both sexes could be induced by male mating behaviour.

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INTRASPECIFIC VARIATION IN QUEEN-MATING FREQUENCY AND SPERM BIAS IN THE ANT *LASIUS NIGER*

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Queen-mating frequency is known to be highly variable across different species of ants and eusocial bees and wasps. Virtually nothing is known, however, about such variation among populations of the same species of social insect. We present estimates of queen-mating frequency in seven populations of the monogynous ant *Lasius niger*, based on electrophoretic mother-offspring analysis of more than 400 incipient colonies. Both the proportion of single and double matings, and the relative contribution of the two males in colonies with a twice inseminated queen appear to vary consistently among the investigated populations. Skewness in the representation of two males in the offspring of a single queen (sperm bias) appears to be less in populations where multiple mating is more common. Several factors may be responsible for variation in queen-mating frequency across populations: 1. The sex ratio of the mating swarm, which is known to be variable in *Lasius niger*. 2. Control of the mating process by flying queens, for whom the benefit of a second mating should be larger than the cost. 3. The fitness interests of males, which depend on the likelihood that colonies headed by double mated queens will ultimately invest in female reproductives or worker-produced males.

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POPULATION STRUCTURE, LOCAL MATE COMPETITION AND SEX ALLOCATION PATTERNS IN THE ANT *MESSOR ACICULATUS*

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Population genetic structure and sex allocation ratios were investigated for the ant *Messor aciculatus* that conducts mass nuptial flights. An electrophoretic survey on two polymorphic loci revealed excessive homozygosities in two populations. Because inbreeding inside the nests was not the case, these heterozygote deficiencies seemed to result from a population subdivision rather than assortative inbreeding during nuptial flights. When no inbreeding was supposed, a simulation, which based on the observed genotype distribution in the study site, suggested that, on average, a breeding swarm consists of alates from only 1.7 colonies. This population subdivision seemed to cause local mate competition (LMC) which can shift population sex ratio toward females. Sex allocation ratio to males in the population (0.166 ± 0.030 ; mean \pm S.E.) was significantly female biased from both the optimum for queens (0.5) and for workers (0.25) without LMC. In addition, sex-ratio variability among colonies was explained well by a pattern of constant male investment predicted under LMC. Thus, the study provides the first evidence of female-biased sex ratio by LMC in ants, contrary to previous assumptions about swarming ants. The results also indicated that LMC can affect sex allocation patterns of individual colonies.

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PRIMARY AND SECONDARY SEX RATIOS IN ANTS: ROLE OF THE QUEEN AND THE WORKERS

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The queen-worker conflicts over sex ratio of reproductive offspring in social Hymenoptera play an instrumental role in theoretical and empirical considerations of the evolution and maintenance of insect sociality. So far, these conflicts have been mainly evaluated by measuring resource allocation to both sexes. A rather straight forward method to measure the extent to which workers and queens respectively control the numerical sex ratio is to compare the primary sex ratio, the ratio of haploid (male) eggs to diploid (female) eggs laid by the queens, to the secondary sex ratio, the ratio of sexuals reared by the colony. This relationship is examined in mature colonies of three ant species very different with respect to their social structure and their behavioral ecology: the Argentine ant *Linepithema humile*, the fire ant *Solenopsis invicta* and *Pheidole pallidula*. In each case, the proportion of haploid eggs laid by the queen(s) is far higher than the proportion of adult males reared by the workers. This difference strongly suggests that workers exert a control on the secondary sex ratio by selective elimination of male larvae. Although such data are consistent with workers preferring a more female-biased sex ratio than queens, the magnitude of the workers influence may also depend upon the primary sex ratio produced by the queen. This is clearly shown in monogyne colonies of the fire ant *S. invicta*, in which colonies may produce adult sexuals of almost exclusively one sex or the other. The comparison of the primary sex ratio between colonies producing sexuals that were almost exclusively male (male-producing colonies) and colonies whose sexuals were almost all female (female-producing colonies) reveals that queens of male-producing colonies lay about two times more haploid eggs than queens of female-producing colonies. In this species, highly male-biased secondary sex ratios produced by workers in relation to more male-biased primary sex ratios may be due to ergonomic constraints that could limit the ability of workers to skew the sex investment.

SOCIOGENETIC ORGANIZATION AND GENE FLOW IN RED ANTS

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Gene flow among populations is an effective means to oppose genetic differentiation generated by mutation, genetic drift, selection and bottlenecking. In ants there is a strong association between the sociogenetic organization of the species and means of dispersal. Monogynous species generally take part in mating flights and found new colonies independently, whereas in polygynous species females often mate within or close to the mother colony and colonies are founded by budding^{1,2}. This leads to different expectations concerning distribution of genetic variation. Monogyny associated with a mating flight should promote sufficient gene flow and uniform distribution of allele frequencies in large areas, whereas in polygynous species dispersal is often restricted and allele frequencies may cluster spatially.

The amount of gene flow was studied in two red ant species, *Myrmica ruginodis* and *M. rubra*. *M. rubra* has usually highly polygynous colonies, whereas *M. ruginodis* is one of the most monogynous species of the genus. Differentiation between populations was estimated from the allele frequency data using Wright's F-statistics³. Differentiation was estimated both in local scale (between sites, within dispersal distance of individuals) and between localities further apart. The differentiation patterns in the two species were clearly distinct. F_{st} values were an order of magnitude larger in the polygynous *M. rubra* ($F_{st} = 0.205$ between sites, 0.199 between localities) than in the mainly monogynous *M. ruginodis* ($F_{st} = 0.027$ and 0.014 between sites, 0.009 between localities). Thus, assuming the island model much less gene flow occurs between neighboring *M. rubra* sites. This agrees with the emerging trend that polygynous and polydomous colonies can in general have very little gene flow between them.

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BIOLOGY OF HALICTINE BEES

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Of the currently recognized 10-15 independent evolutionary events of eusociality among insects, at least four occurred in lineages belonging to a single group of bees, the sweat bee subfamily Halictinae. This cosmopolitan subfamily comprises about 4000 described species, many of them solitary, but overall exhibiting a remarkable diversity in social organization and life history. Various forms of sociality - including communal, semisocial, primitively eusocial, and perennially eusocial - have arisen multiply among the Halictinae. Likewise, reversals from social to solitary life have evolved repeatedly. Because of this unparalleled evolutionary plasticity in social organization, the Halictinae represent a choice taxon for phylogenetic, ecological, and behavioral investigations into the selective factors modulating the evolutionary origin and maintenance of sociality. It is surprising therefore that sweat bees have received less attention than other social insects. Even though the ecology and behavior of a few select species have been studied in great detail, the basic biology of many sweat bee lineages remains unknown. Similarly, phylogenetic relationships among major lineages are poorly resolved. This dearth of information partially stems from the difficulty in studying sweat bees with their concealed nests (nesting in soil or rotting wood) and small body size (making individual marking and tracking difficult), but these disadvantages are compensated for by the relatively small colony sizes (allowing detailed behavioral studies of all colony members) and frequent occurrence in large nest aggregations (facilitating sampling of many nests and individuals). This symposium presents exemplary studies that have capitalized on the advantages of studying sweat bees and that involve all aspects of halictine biology, including phylogenetic history, sociality, mating systems, parasitism, and chemical ecology. It is our hope that the present symposium will help to outline future directions and stimulate further research on this unique group of social insects.

EUSOCIALITY IN BEES: THE MAIN STAGES, TRENDS AND CONSTRAINTS OF THE EVOLUTION

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Subsocial way to eusociality is considered by us as only possible. The following biological features of a bee species are necessary prerequisites for the appearance of eusociality: monoandry of females, their ability to control sex of offspring, to distinguish fertilized and non-fertilized eggs, to distinguish related and unrelated individuals, also care for a brood by a female, long period of egg-laying, temporary help to a mother by daughters. Eight stages of the evolution of eusociality in bees are ascertained: **I. Primitive-subsocial stage:** (1) care for the brood by a solitary female, (2) long period of egg-laying.— Many *Halictinae*, *Xylocopinae*, *Euglossinae* and possibly *Nomiinae*. **II. Eosocial stage:** temporary help to the female by her daughters till founding of own nests by them.— *Evylaeus villosulus*, *Xylocopa sonora*, *Eulaema nigrita*. **III. Transitional stage** (appearance of facultative and very primitive eusociality): (1) some daughters remain with their mother and do not mate, (2) these daughters build cells in which their mother lays eggs, (3) the daughters partly replace unfertilized eggs layed by their mother with their own eggs, etc.— *Evylaeus albipes*, *E.rhytidophorus*, *Seladonia confusa*, *Augochlorella striata*, *Augochloropsis sparsilis*, *Pseudaugochloropsis nigerrima*, *Ceratina japonica*, *C.okinawana*, *Xylocopa combusta*, *X.pubescens*, *X.sulcatipes*, *Euglossa cordata*. **IV. Lower primitive-eusocial stage** (stabilization of eusocial life and its expanding to the whole population or species): (1) reduction of the first (worker) brood, (2) decrease in the proportion of males in a worker brood, etc.— *Evylaeus laticeps*, *E.versatus*, *E.zephyrus*, many *Allodapini*. **V. Middle primitive-eusocial stage** (colony integration): (1) disappearance of males in a worker brood, (2) intensification of parental manipulation, (3) non-overlapping morphological differentiation of castes.— *Evylaeus cinctipes*, *E.linearis*, *E.umbripennis*, *Seladonia hespera*. **VI. Mature primitive-eusocial stage** (increase in the efficiency of life by a colony): (1) increase in the number of worker broods, (2) all colonies are founded monogynously, etc.— *Evylaeus malachurus* and *E.pauillus*. **VII. Higher primitive-eusocial stage** (transitive to advanced-eusocial): (1) continuous rearing of offspring during a season, (2) making reserves of food, (3) termoregulation of a colony and incubation of a brood, etc.— *Bombus*. **VIII. Advanced-eusocial stage** (colony living for ever): (1) colony foundation only by swarming, (2) obligate age polyethism, (3) communication and information channels of management of family, etc.— *Meliponinae* and *Apinae*. The main constraints and prospects for the evolution of eusociality at *Halictinae*, *Xylocopinae*, *Euglossinae*, and *Bombinae* are discussed.

PHYLOGENY OF THE HALICTIDAE AND ORIGINS OF EUSOCIALITY

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Cladistic analysis of morphological data confirms that the Rophitinae (=Dufoureaeinae) is the sister group to the Nomiinae+Halictinae, but does not identify which other bee families are most closely related to the Halictidae. The Halictidae are united only by mouthpart characters. Within the Halictinae, the Nomioidini is the sister group to the Augochlorini+Halictini. Communal behavior is an evolutionary alternative to caste-based semisociality and eusociality, having evolved in separate phylogenetic lineages, especially in the Nomiinae, the Nomioidini, the *Agapostemon* complex, and the Australian Halictini. Our phylogenetic analysis of the Augochlorini indicates that eusociality evolved separately from that in the Halictini and probably evolved just once, in the *Augochlora* complex of genera. We also found evidence of a single reversal to solitary nesting in *Augochlora* s.s. Semisociality occurs in the most basal lineages of Augochlorini, suggesting that it may be plesiomorphic for the tribe. In the Halictini, phylogenetic analyses using allozymes by Richards and Packer indicate that eusociality is primitive in *Halictus* s.l. and also in the carinate *Evyllaes*, with several reversals to solitary nesting. *Dialictus* remains unresolved phylogenetically, with perhaps two or more independent origins of eusociality. Single apparently eusocial nests have been described from two African *Lasioglossum* s.l. species. Conservatively, eusociality has evolved 4 to 7 times independently in the Halictidae.

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Communal Sociality in Australian *Lasioglossum*

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Australian species in the genus *Lasioglossum* are communal. One such species, *Lasioglossum (Chilalictus) hemichalceum*, is widely distributed in southeastern regions. Laboratory and field studies conducted in Cobbonnee State Forest in southwestern Victoria have shown that this species is highly cooperative. It is bivoltine and nests are used for more than one year suggesting that colonies are long lasting. Males are dimorphic. One morph is small and morphologically similar to other halictine males while other morph is much larger, and has a strikingly oversized head and mandibles and undersized wings. These macrocephalic males do not fly, but remain in nests where they fight one another, often to the death, and mate with resident females. Group members are highly cooperative but are not more cooperative toward familiar than unfamiliar individuals. Females exchange nectar via oral trophallaxis, and behave cooperatively in laboratory experiments. They are more cooperative than either solitary or eusocial species of *Lasioglossum*. Finally, unrelated individuals construct tunnels cooperatively and may provision cells cooperatively. Relatedness estimates, based on two variable isozymes, indicate that overall relatedness is low, and that the females in reproductively active colonies are not relatives. This is remarkable given that females in a colony could be the daughters of the same male. Additional studies of *L. hemichalceum* will focus on two major questions. Why are they cooperative, i.e. what is the advantage of group life; and how is cooperation maintained, i.e. what mechanisms are in place to prevent cheating.

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EVYLAEUS ALBIPES (F.) (HYM., HALICTINAE): AN EXAMPLE OF DIRECT PASSAGE FROM SOLITARY LIFE TO EUSOCIALITY.

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Evyllaesus albipes is a Palearctic species extending from Ireland to Japan, widespread in the North, but living mainly in hilly regions in the South. Most populations - including that found in eastern France which is studied both in the field and in the laboratory - show a solitary cycle. Some populations, from the Parisian region and south-western France, present a non-delayed eusocial cycle, with a first brood composed of workers and males. It has been confirmed by laboratory research that workers and foundresses belong to two distinct castes. Workers are immediately active on emerging; groups of orphan worker pupae develop into small summer societies with division of labour. Future foundresses become active only after overwintering. The difference between the solitary and the social cycles lies in the presence or absence of an additional brood of workers. The other biological characteristics are common to the whole species: reopening and inspection of the brood cells, facultative polygyny (semisociality) and delayed eusociality. *E. albipes* presents, like *E. calceatus*, an example of direct passage, in allopatry, from solitary to eusocial life.

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HAPLODIPLOIDY, SUBFERTILITY, ASSURED FITNESS RETURNS, AND THE EVOLUTION OF EUSOCIALITY IN THE SWEAT BEE *AUGOCHLORELLA STRIATA*

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Detailed field observations over three years on the primitively eusocial sweat bee *Augochlorella striata* (Halictidae) allowed weighing of the relative importance of intrinsic factors (relatedness asymmetries) and extrinsic factors (ecological constraints) in the maintenance of eusociality in this species. Experimental manipulation of relatedness asymmetries revealed facultative sex-ratio biasing by workers and thus implicated the role of haplodiploidy in the evolution of worker behavior. Female-biased sex ratios and a 3:1 relatedness asymmetry augmented the inclusive fitness of workers by 5-10%. 60-80% of the inclusive fitness of workers accrued via indirect reproduction (working for a mother- or sister-queen) and irrespective of female-biased sex ratios; the remaining inclusive fitness accrued via direct reproduction (superseding the mother queen, producing sons). The inclusive fitness of independently reproducing, solitary foundresses was only 1.4-1.9 times greater than the inclusive fitness of workers, because of high mortality of solitary foundresses and low mortality of established colonies. However, this fitness comparison was confounded by size differences between workers and foundresses and the fact that foundress fitness was positively correlated with foundress size. The positive correlation was due to greater mortality of smaller foundresses during nest initiation, and greater work forces and greater reproductive output of colonies headed by larger foundresses. These findings suggest that eusociality in *A. striata* is maintained by a combination of multiple factors, most notably the interaction of "assured fitness returns" accrued by workers and ecological constraints causing subfertility of small independently reproducing females. Fitness gains due to sex-ratio biasing and haplodiploidy appear of secondary importance, but may contribute to the maintenance of eusociality.

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DELAYED EUSOCIALITY IN HALICTINE BEES

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Almost all eusocial halictine bees have an annual colony cycle in which overwintered females initiate a nest (either alone or in a small semisocial society) and produce one or more broods of workers. The colonies die out at the end of summer. One exception to this rule is well known: *Lasioglossum (Evyllaesus) marginatum* has perennial colonies with one worker brood a year for five years before male and next generation gynes are produced (Plateaux-Quénu, 1959, *Année Biologique*, 35:235-444).

In 1957 the senior author commenced a long term study of a Japanese species *Lasioglossum (Dialictus) problematicum* (Sakagami, 1979, *Anima*, 79:54-59). In this species, many nests are occupied only by one solitary female. However, multi-female nests also occur and these are of two types: semisocial colonies made up of sisters that overwintered together and delayed eusocial colonies in which one or more daughters coexist with their mother in the second year of her life. The relative frequency of these colony types varies between sites and between years.

More recently, survival of females into a second year has been documented for two closely related species of the subgenus *Evyllaesus* - *Lasioglossum (Evyllaesus) fratellum* (von der Heide, 1992, *Drosophila* 92:171-188) and *L. (E.) comagenense* and in both species solitary, semisocial and eusocial nests occur.

In this talk the nature of delayed eusocial societies will be discussed. They are difficult to detect but offer some spectacular advantages to students of insect sociobiology.

THE RELEVANCE OF MATE RECOGNITION TO
THE EVOLUTION OF SOCIALITY IN SWEAT BEES
(HYMENOPTERA: HALICTIDAE)

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Traditionally, biologists interested in insect sociality have ignored the behavior of males, viewing them as "ethological non-entities" (1). Slowly this parochial view is being corrected. More recently, for example, Hölldobler and Michener (2) hypothesized that male mate recognition systems in solitary taxa might represent the evolutionary origin of kin recognition systems used in eusocial taxa (3). Others have attempted to link male behavior to sociality via mating as a mechanism for caste determination (4,5).

Bioassays show that individually-distinctive female odors (3,6; Ayasse, this symposium) are olfactory cues used by males to localize and recognize females in the eusocial sweat bee, *Lasioglossum (Dialictus) zephyrum*, and the solitary *L. (D.) figueresi* (Halictini) (3,6), the solitary *Dieunomia triangulifera* (Nomiinae) (3), and a parasitic bee, *Paralictus asteris* (Halictini) (in prep.). Furthermore, bioassays show that males learn these odors, and modify their behavior appropriately to avoid repeated attempts at mating with unreceptive females. There is no evidence to suggest that males are preferentially attracted either to novel females or to females from the same nesting site. Some evidence indicates that there are costs to repeated attempts at mating by males. Females invest much effort in producing offspring, while males provide no investment other than at the time of mating. Patterns of parental investment suggest that sexual selection for refined discriminating abilities is likely to be less intense on males than on females.

Strong tests of the above hypotheses are precluded by the limited comparative information, and by the lack of information on phylogenetic patterns, but available studies indicate that further investigations are warranted.

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THE MEANING OF MALE ODOR IN THE MATING BIOLOGY OF SWEAT BEES (Hymenoptera: Halictidae)

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While several investigations and behavioral experiments showed that sex pheromones of female bees attract males and stimulate copulatory behavior, there is not very much known about the function of male odor compounds involved in the mating behavior. In the primitively eusocial sweat bee *Lasioglossum malachurum*, the role of male odor in copulatory behavior was examined by behavioral experiments and chemical analysis.

Behavioral experiments with odor extracts of males and synthetic compounds demonstrate that male odor released during mating has an inhibitory effect on the copulatory behavior of conspecific males (Ayasse, 1991). Hexadecyl octadecenoate, a wax-type ester that has been identified as a main compound in cuticular washings of males (85%), seems to play an important role. The inhibitory effect was even stronger, when a species-specific mixture of hydrocarbons was added. Odor of males from a foreign population showed a weaker inhibitory effect in comparison to cuticular washings of males collected from the target population. A comparison of the absolute amount of volatiles on the cuticular surface of virgin and just-mated queens showed that females were not impregnated with male odor. The assumption that odor is emitted during copulation only, is supported by headspace samples of copulating bees: A larger amount of hexadecyl octadecenoate was present in copulating bees as compared to samples of males or attractive young queens. A diminished attractiveness of mated young queens may be the result of a quick change in the secretory odor after mating (Ayasse et al., 1993). The odor signal released by the male during copulation could provide conspecific males with information about the mating status of a female.

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CHEMICAL ECOLOGY AND HOST RELATIONSHIPS OF
SHECODES NEST PARASITESJ. Tengö¹ and H. Sick²

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Finding host nest areas, host nests, and intruding successfully into host nests are prerequisites of reproduction in parasitic bees. The aim of our study was to connect the nest searching strategies of kleptoparasitic *Sphecodes* females, their nest intruding and intranidal behavior with the chemical ecology of host and parasite. Individually marked *S. ephippius* and *S. pellucidus* females showed a large searching radius, enclosing several host nest areas. Compared to host specific *Nomada* females, they neither guarded hosts nests nor learned their location within the nest areas. Nest invasion strategies were studied in six *Sphecodes* species, having social and/or solitary halictid hosts. Females always preferred to enter unguarded nests; only *S. monilicornis* females were seen to enter nests aggressively during the social stage of their host, *Lasiglossum melschurum*. Having gained control over a social host nest enabled the parasite to lay a large number of eggs in a short period as could be observed in laboratory nests between glass sheets. GC-MS analysis of host and parasite Dufour's gland extracts revealed species specific patterns and supported the behavioral observations: chemical mimetism by a single characteristic component common to host and parasite, as in *Nomada*, could be excluded. Comparison of the whole bouquet of all species by a Wagner parsimony procedure resulted in a separation of hosts from parasites. Within the genus *Sphecodes*, two groups could be distinguished by their Dufour's gland secretion composition (mainly hydrocarbons) and Dufour's gland morphology. This result corresponds to those found in morphological studies by several authors.

LEARNING AND MEMORY: COGNITION IN SOCIAL INSECTS?

Organizers: C. Masson and M. Lehrer

Social insects must cope with a variety of tasks that solitary insects need not bother about. The members of a colony must act as builders, nurses, soldiers, or foragers, and in some cases one and the same individual takes over each of these tasks at different stages of its life. Many of these activities are innate to the insect, i.e. they are not based on learning processes. At the level of the individual animal, it is mainly the foraging task that requires a flexible behavioural repertoire, and thus an excellent learning capacity. To optimize its foraging success, the insect must remember the route to a foraging site, as well as the route back to the nest. It must, in addition, memorize the appearance and scent of the food source. The question as to how the insect's small brain processes and stores this large amount of information has puzzled neurobiologists for many decades. Some of the amazing performances of social insects have given rise to yet another question, namely whether or not some mental operations might act on the stored information, i.e. whether or not cognitive processes are involved in some of the performances observed. In the light of these questions, our speakers will present recent findings involving various capacities of social insects, learning performances, and brain functions. The presentations are concerned with results of behavioural studies, as well as neurophysiological correlates of the observed behavioural patterns. They include, in addition, aspects of behaviour that can only be explained by considering the insect colony as being a superorganism, coping, by means of an efficient communication system, with a variety of tasks that could not be managed by the individual animal.

Invited participants are:

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COGNITION AND ECOLOGICAL PERFORMANCE: ENERGETIC RATE REPRESENTATION IN FORAGING BUMBLE BEES.

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A cognitive theory of information-processing turns critically on the assumption that external information is translated and represented in the organism's brain through the functioning of specific mental operations. The position necessary for inferring a specific adaptive value to cognitive mechanisms then relies on demonstrating that environmental information can be differentially represented and that the organism represents the information in a manner that increases its likelihood of survival, reproduction, and/or mate acquisition. Over the past several years, we have explored the manner in which individual foraging bumble bees represent the energetic quality of the flowers they visit and how such representation form the basis for floral choice. Information on the energetic rewards obtained from individual flowers of a given species can be assembled into a variety of rate characterizations. In a series of choice experiments, I constructed alternative choices differing in either short-term energetic rate or long-term energetic rate. In all cases, individual foragers select the floral type generating the largest short-term rather than long-term energetic gain. Reliance on short-term rate as the currency of choice is not expected and may depend on limits to memory or to exploitation of spatially structured energetic landscapes within the natural habitat of the bee.

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TIME AND PLACE MEMORIES IN ANTS

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If evidence of temporal learning in temperate species of ants has not been forthcoming (Hölldobler and Wilson, 1990), even after extensive training in 14 European species (Dobrzanski, 1956), it is known that the tropical ant *Paraponera clavata* preferentially forages in the field at the time of production of artificial nectar sources (Harrison and Breed, 1987). This difference could be expected considering the fact that none of the temperate species depends on nectar as a food source which is generally produced only at restricted times of day (Carroll and Janzen, 1973). On the other hand, it is not yet known whether the tropical ants can time stimulus events, i.e. display a memory for time, or just react to changes in the environment, like the daily succession of the sun azimuthal positions, i.e. display a time-dependent memory. Our laboratory data clearly demonstrate that the tropical ants *Ectatomma ruidum* have access to an internal clock, which they can use to record the time of day at which food is to be found on a given site and use this memory to schedule feeding behavior on subsequent days. In addition, a true association between place and time implies that the insect could simultaneously learn and store spatial and temporal information in a joint control of behaviour allowing it to visit different places at specific times of day. Despite the fact that it has been claimed many time that bees are able to perform such a true time-place learning (Beling, 1929; Koltermann, 1974), even when bees were trained to feed at two (Wahl, 1932) or four (von Frisch, 1965) different places at two or four restricted times of day, no convincing evidence with individual bees have been provided to this date (Biebach et al., 1989). Their temporal learning performances could have been simply based on an entrainment of their circadian system by the feeding schedule (Aschoff, 1986; Frisch and Aschoff, 1987). We tested in laboratory conditions whether an association between temporal and spatial changes in the daily pattern of sugar sources availability can be learned by the neotropical ant *E. ruidum*. Honey was alternately and intermittently available at one among three feeding sites to which the insects had continuous access. Our data show that individually marked ants rapidly learn to associate a particular site with the specific time at which food is to be found (Schatz et al., 1994). Thus ants do not only rely on immediate reinforcement but also on memory to control their foraging behaviour. In addition, their memory for the time at which food is available is linked to their memory for its location.

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DO BEES BIND THE COMPONENTS OF PANORAMIC PATTERNS?

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Foraging bees learn to recognise patterns which cover large areas of their visual field. In their everyday life they may need to store several such patterns at the same time. Do bees have a mechanism for 'gluing' together the separate parts of an individual pattern? To find out, bees were trained to recognise two separate patterns, each composed of 4 widely spaced components. Tests compared the bees' response to composite patterns, that were constructed out of a mixture of the two patterns, with the insects' response to one of the separate patterns. The results so far indicate that under some conditions bees learn each component of a pattern independently of the others, with no binding between components. Potential confusion between stored patterns is avoided by the existence of powerful contextual cues which mean that a complex pattern that is learnt in one place is not recognised elsewhere.

PERFORMANCE OF HONEYBEES IN ANALOGUES OF THE RODENT RADIAL MAZE

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The performance of individual honeybees pretrained to forage at a laboratory window was studied in three rudimentary analogues of the radial maze used for the study of short-term spatial memory in rats and other vertebrates. A linear array of three targets was used in Experiment 1, a triangular arrangement of three targets in Experiment 2, and a rectangular arrangement of four targets in Experiment 3. In each experiment, there was one trial per visit to the laboratory, with reward only for the first response to each of the targets presented on each visit. A number of systematic patterns of performance were observed, but the results provided no indication that the behavior of the animals was influenced by memory of targets recently exploited -- no evidence, that is, of short-term spatial memory.

CONDITIONS FOR GOAL-ORIENTED BEHAVIOUR IN HONEYBEES

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Insects use several references to orient toward distant goals. Most pronounced among these are the sun compass [1], landmarks in relation to the sun compass and to each other [2], and a path integration mechanism [3]. In most displacement experiments, honeybee foragers released at novel sites flew into the sun compass direction [4]. We thus consider the sun compass as the dominant factor in a multifactorial, hierarchically organised set of mechanisms. In some instances, displaced foragers flew into the goal's direction from the release site [5, 6]. Such behaviour was interpreted as an indication of a geometric representation of space in form of a cognitive map [6]. We have examined under which conditions displaced bees approach a goal from a novel release site, and which mechanisms might be involved. Our results show that a hierarchy of interacting orientation reference mechanisms leads the bee to choose a particular direction as the most probable one leading to the goal. These mechanisms may be based on external cues (sun compass, landmarks) or internal conditions (memory, motivational state). External references may compete with each other, and the outcome of this competition also depends on internal conditions. Thus, a) bees will orient in the sun compass direction if the horizon profile and landmark layout at the release site is different from the previously learned situation and if they are strongly motivated to fly toward their goal, and if celestial cues or obvious landmarks learned relative to the sun compass are available; b) repeated releases at the same release site increase the probability of orientation directly toward the goal by means of context specific memory retrieval and path integration; and c) orientation toward a landmark signalling the goal which is seen in a novel direction from the release site may occur if other, stronger references are not available. During the flight of a foraging bee, several to many memories are formed which are retrieved specifically and which compete with each other upon release. We conclude that the multiple set of orientation mechanisms is sufficient to explain goal-oriented behaviour in the bee without the necessity to assume operations at the level of a geometric representation of space (cognitive map).

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HOW HONEYBEES ACTIVELY ACQUIRE DEPTH CUES

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As opposed to many vertebrates, most insects possess no specific mechanisms for depth perception, such as binocular stereopsis or accommodation of the lens. In the task of estimating the distance of an object, the bee has been shown to use, instead, either the object's apparent size (a near object subtends a larger angle on the eye than a more distant object), or the speed at which the object's image moves on the eye during the insect's free locomotion (a near object moves faster than a more distant one, irrespective of its size). More recent studies provide evidence that the bee extracts depth cues from image motion by actively creating the optic flow that can provide distance information. We found two types of flight patterns, both performed at the feeding site, that do not serve for locomotion *per se*, but rather represent two different strategies for active acquisition of information on absolute distance. One is based on a learning process, i.e. the bee modifies her flight behaviour as soon as she has learned that the task can only be coped with by using depth cues. In this case, depth information is acquired on arrival at the food source and is used for as long as the bee keeps visiting that food source. The other strategy is based on a stereotype flight pattern which is innate to the bee's behavioural repertoire. In this case, depth cues are acquired upon departure from the food source, and are used only during the first several visits of the bee at a novel food source. Both of these strategies for active acquisition of depth information have probably evolved in the context of the social insect's need to optimize its foraging success.

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WHENCE COGNITION IN SOCIAL INSECTS? IS IT AN INDIVIDUAL OR A SUPRA-INDIVIDUAL PHENOMENON?

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Any definition of cognition must involve the degree of flexibility in linkage of sensory, central and motor systems as well as internalization of information such that stimuli need not be present in the immediate environment to invoke a response. Critical factors in the Central Nervous System that limit the qualities that this representation can attain are numbers of cells and how those cells are interconnected. An individual honey bee's CNS contain on the order of 10^6 neurons, while that of larger mammals contains 10^9 – 10^{12} . Assuming that the average connectivity is the same, then from cell count alone one would suspect vast differences in the ability to represent information. Indeed, there is no unequivocal evidence in honey bees that complex internal representations exist. Instead, the flexibility of individual bees in their behavior can be accounted for by less complex models of learning (Menzel 1990; Smith 1993). However, to focus solely on the performance of individuals ignores the mutualistic communication that takes place within a colony (Markl 1985). 10^4 bees in a small colony contain collectively 10^{10} neurons, although the *connectivity* among individuals is bound to be much more constraining than if the neurons were to reside in a single brain. Nevertheless, responses to stimuli by distributing information among individuals imparts greater flexibility, which can in part be shaped by genotypic differences among individuals. Important questions must now regard how "social" connectivity influences information processing and what emergent properties involving learning phenotypes can be identified at the level of the colony.

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FLOWER FORM RECOGNITION AND COLOUR INFORMATION IN THE HONEYBEE

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Experiments on honeybee pattern recognition have been mostly performed with abstract forms (see [1] for review) and led to the conclusion that pattern recognition may be achieved either on the basis of parameters such as content of high spatial frequencies (see [1] for review) or using eidetic images that are compared to the patterns currently seen [2]. Both hypothesis are not, however, exclusive and it is not yet clear when bees may use one strategy or the other. It was also claimed that pattern recognition in the honeybee implies some kind of cognitive abilities like concept formation [3]. In our case, we wanted to study as closely as possible natural conditions under which freely-flying bees learn and discriminate flower forms. In particular, our work was designed to find out 1) whether bees can discriminate different angular orientations of a bilaterally symmetrical flower form, 2) whether they can distinguish variations of the same flower form in which only symmetry was varied by changing the angular orientation of its petals, and 3) whether the colour of the stimulus affects flower form recognition. Honeybees (*Apis mellifera*) were trained to a bilaterally symmetrical flower form presented vertically on a patch allowing the acoustical recording of bee choices by means of invisible microphones in the centres of the stimuli. Multiple choice tests with twelve alternatives were performed after bees reached the asymptote of the learning curve. We demonstrated that: 1) bees actually discriminate the different orientations of the same flower figure on the basis of an eidetic image, with the lower visual field being more highly weighted in the matching task; 2) bees confronted with different symmetry alternatives can distinguish the trained stimulus from the alternatives; recognition seems also to be based on a matching strategy prioritizing the overlapping in the lower visual field but also on an evaluation of symmetry in case of ambiguities after the matching strategy; 3) the colour of the stimuli influences the choice behaviour. When colour contrast to the background is reduced, bees seem to rely more on their pattern recognition system. This supports the notion of a hierarchical organisation of colour and form perception in the honeybee, where the former dominates over the latter. This could be simply due to differences in the visual resolution and detection capabilities of the honeybee. Our results thus suggest that form recognition in honeybees is accomplished by means of simple strategies without the necessity of assuming higher cognitive levels.

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OLFACTORY FEATURE EXTRACTION AND SENSORY MEMORY IN THE BEE: EXPERIMENTAL AND MODELLING APPROACH

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Honeybee foraging behaviour is strongly based on discrimination among complex odours which is the result of a memory process involving storage and recall of "key-features" representative of the plant aroma. The study of the neural correlates of such mechanisms requires a determination of how the olfactory system successively analyses odours at each stage of the network. A comparison of the successive 'olfactory images' is particularly well performed through our modelling approach. All studies suggest the implication of both antennal lobe and mushroom bodies in these processes. The antennal lobe would be the location of noise reduction, feature extraction and sensory memory, thus allowing the consolidation of the memory trace in the mushroom bodies. We studied the computational capacities of the neural circuitry in the antennal lobe and proposed a simple scheme for sensory memory. The model predicts the representation of key-features supported by spatial activity maps. Moreover, modulation of lateral inhibition enables the antennal lobe network to memorize the neural activity pattern after stimulus offset.

In agreement with physiological and behavioural data, we propose a working hypothesis for further modelling approaches in order to study the different memory phases and their relative locations and time scales.

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4-METHYL-3-HEPTANONE: A PARADIGM OF ALLOMONAL-PHEROMONES IN THE HYMENOPTERA

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The ethyl ketone 4-methyl-3-heptanone appears to be one the most widely distributed semiochemicals produced by species in a variety of subfamilies in the Formicidae. This compound is characteristic of diverse natural products in being simultaneously a pheromone and an allomone as a significant example of *exocrine parsimony*. The pheromonal role of this ketone is frequently utilized in a defensive context as is the case for a variety of other eusocial allomonal pheromones. Thus there are no strong grounds for arbitrarily assigning pheromonal or allomonal functions for many exocrine compounds. This view is reinforced by the fact that compounds such as 4-methyl-3-heptanone are produced in the inordinately high concentrations that are characteristic of defensive allomones. In some cases the purely allomonal role of 4-methyl-3-heptanone is clearly evident in the noneusocial species that utilize this ketone as a contact deterrent. Eusocial species can utilize their defensive allomones in a variety of ways unrelated to predator deterrence. The defensive system of the Asiatic ponerine *Harpegnathos saltator* will be described in order to illustrate the elegance of this allomonal-pheromonal system.

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DEFENCE COMPOUNDS IN SOCIAL INSECTS : A MEANS OF EQUILIBRIUM IN ECOSYSTEMS AND MECHANISMS OF EVOLUTION.

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In the temperate ecosystems of Europe and North America, there exist predatory ant species whose preys are the *Reticulitermes* termites. The termite soldiers synthesize terpenes as a means of defence against their predators¹. The quantities of this venom synthesised depend on its efficiency against the particular ants inhabiting each part of the ecosystem : a process of natural selection has led to a quantitative adaptation to the level of ant predation encountered. The strategies used by the predators vary depending on their resistance to the soldiers toxins. The *Pheidole* ants carry out raids and are highly sensitive to these terpenes as are the *Ponera* ants, which make use of a chemical mimetic strategy. The *Monomorium* ants, which are highly resistant to termite terpenes such as Geranyl-linalool, kill the termites by depositing alkaloids on their cuticle using their spatulate sting². Ants such as *Leptothorax* and *Myrmica* have a medium level of sensitivity to the termite soldiers' terpenes. All these chemical interactions contribute to the equilibrium of the ecosystems and to regulating the numbers of the social insects inhabiting the forests creating, probably, more diversity.

In several sympatric *Reticulitermes* termite species in U.S.³, their soldiers have been found to secrete different terpenes which act in different ways. This phenomenon can probably be accounted for in terms of differential ecological niche occupation.

The variations to which social insects' defensive and offensive substances are subject constitute useful models for studying evolutionary mechanisms. Identifying the molecular targets of toxins and elucidating the detoxifying mechanisms involved should make it possible to perform comparative studies on the efficiency of the diverse molecules secreted by the various actors involved in forest ecosystems.

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SYNTHETIC AND BIOSYNTHETIC STUDIES OF ANT VENOM ALKALOIDS.

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Several years ago we reported that the poison gland of the New Guinea pseudomyrmecine ant *Tetraponera* sp. contains a series of new alkaloids for which the name tetraponerines was coined. The structure of the major alkaloid, tetraponerine 8 (T8), possessing the unprecedented 6-alkyldecahydropyrido[1,2-c]pyrrolo[1',2'-a]pyrimidine skeleton, was established by an X ray diffraction analysis¹. The structures of five other tetraponerines (T3 to T7) were proposed on the basis of their spectroscopic properties². Several syntheses of (±)- and (+)-T8 have been recently published³. The unusual structures and biological properties of the tetraponerines prompted us to study their absolute configuration, their biosynthesis and their pharmacological activities. With this end in view, we have developed new syntheses of racemic and of enantiomerically pure tetraponerines, among others, 9-epi T8. This allowed us to correct the relative configuration proposed for T3 and T7. On the other hand, administration of ¹⁴C labelled precursors to the ants and chemical degradation of the radioactive T8 favour the hypothesis that the pyrrolidine ring of T8 is derived from L-glutamic acid via L-ornithine and putrescine, while the other part of the molecule (a twelve carbon chain) comes from the combination of six acetate units.

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DEFENSE CHEMISTRY IN AN ANT-TERMITE RELATIONSHIP

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We report on the chemistry and function of poison gland constituents of the ant *Myrmicaria eumenoides* and the defense chemistry of the termite *Schedorhinotermes lamanianus*. The poison gland secretion of foragers of the ant is mainly made up by a low boiling monoterpene, (+)-limonene, and a mixture of (3*R*,5*R*,8*aS*)-3-butyl-5-propionyloctahydroindolizine and its (5*S*)-diastereomer which we like to call Myrmicarins A und B. These compounds are structurally related to the Monomorphins known from pharaoh's ants and to some alkaloids known from poison dart frogs, *Dendrobates* spp.

Both the low boiling and the high boiling fraction of the ants' poison gland show at least a dual function. The terpene serves physically as a solvent and a spreading factor for the alkaloid when smeared on the cuticle of arthropod preys or enemies, while physiologically it acts as a short-range-recruitment signal. The alkaloids, besides their physiological properties as poisons, serve physically as fixatives or keepers for the low boiling terpene fraction [1].

Sibling species seem to follow the same principle by producing mixtures of monoterpene hydrocarbons and alkaloids.

Frontal glands of the termite soldiers contain large amounts of straight chain vinylketones [2] and β -ketoaldehydes showing 14 and 16 carbon atoms along with small amounts of biogenetically related compounds. These highly reactive substances may block physiologically (chemo)-receptors of the aggressor or they may act physically as a glue after application and polymerisation. The defense secretion of the termite inhibits both short-range- and long-range-recruitment behavior of the ants.

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MECHANISM OF ACTION OF A DIALKYLPIRROLIDINE FROM ANTS ON INVERTEBRATE NERVOUS SYSTEM

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Ants from the genus *Monomorium* are natural predators of termites from the genus *Reticulitermes*. The efficacy of their raids against termites is principally due to the use of a paralyzing venom, that they deposit on the cuticle of their prey with their spatulated sting apparatus. Several dialkyl-pyrrolidines and 2-Methyl-6-alkyl-piperidines have been identified in this venom and revealed a wide spectrum insecticidal activity. The mechanism of action of dialkyl-pyrrolidines has been assessed on two types of *in vitro* nerve preparations from the crayfish *Procambarus clarkii*. 2-(1non-8enyl)-5(1non-8enyl)-pyrrolidine (Pyr 9) was shown to block nerve conduction when applied topically on nerves through a lipophilic interface. Experiments performed on voltage clamped axons clearly demonstrated that this blockade was due to the inhibition of sodium currents. The mechanism of action on sodium channels appeared similar to that of local anaesthetics, with both a tonic and a phasic block, and a shift of the inactivation curve towards more hyperpolarized potentials. The inhibitory action of Pyr 9 on sodium currents seems to account for the knock down effect of dialkylpyrrolidines on topically treated insects.

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SOCIAL INSECT ALLOMONES and STEREOCHEMISTRY

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In general, allomones are only produced in trace amounts and are rarely proved to be solids amenable to X-Ray crystallography, and their identifications have generally required degradative research in combinaison with a variety of spectral techniques, especially G.C.M.S. (Gaz Chromatography Mass Spectrometry). To the end, synthesis becomes a *sine qua non* of the investigative process when question of relative stereochemistry need to be answered¹. But to day the determination of their absolute configurations is still the major problem to solve, in a next future this question will certainly received an answer due to the tremendous progress of the asymmetric synthesis. Pyrrolizidine alkaloids offer attractive targets for synthesis because of their structures and biological activities like xenovenine which have been isolated from ant venom (*Solenopsis xenovenenum*). Meanwhile the structure and relative stereochemistry have been established as (5Z, 8E)-3-heptyl-5-methylpyrrolizidine². Herein we present an enantiospecific synthesis of the two enantiomers starting from the same chiral source the (S)-pyroglutamic acid. Using analytical methods these isomers constitute the indispensable material to compare with the natural product and to establish his absolute configuration.

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ARTHROPOD DEFENSIVE SUBSTANCES AS NEUROTOXINS AND REPELLENT AGENTS.

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Arthropods synthesize a dazzling array of chemical compounds, used in various interactions with other organisms, such as defense against predators or competitors, predation and protection against pathogens. But, although the structures of many compounds have been identified, too often little is known about their complex biological roles. The study of chemical interactions between arthropods may help us understand better the significance of chemical signals in the ecological web, and may also provide us with useful leads for the development of novel agrochemical or pharmaceutical agents. Considering the achievements of modern analytical chemistry, the bottleneck for the study of bioactive compounds is often on the biological side: the amounts of compounds produced are often a limiting step for the isolation of active substances. Therefore a number of microtechniques for the study of the toxic activity of arthropod defensive secretions have been developed. These include behavioral assays (repellency), topical application, microinjection and microscale physiological assays. In particular, we developed the latest two methods for the isolation of neurotoxic components in scorpions, centipedes, wasps, and ants venoms. Microinjections using *Drosophila melanogaster* were done with glass pipettes, for injection volumes of 50nl or less. A microchamber of 100ul was developed for an insect smooth muscle preparation. We have also extensively studied the toxicity of ant alkaloids in the genres *Monomorium* and *Solenopsis* (dialkylpyrrolidines and -piperidines) and demonstrated clear structure-activity relationships in a series of natural and synthetic compounds, which act as neurotoxins and show considerable contact toxicity against termites and other insects. The allomonal secretions of arthropods represent a unique, barely explored, source of bioactive compounds, and this review will focus on their potential, showing the importance of the understanding of ecological interactions and a multidisciplinary approach to this study.

DEFENSIVE MODES OF ACTION OF HYMENOPTEROUS VENOMS

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Hymenoptera are small. Vertebrates are large. These characteristics plus the rich nest food resources often available to predators place aculeate Hymenoptera in a unique situation vis-a-vis defense. No other insects are in positions of such intense, long-term predation pressure by enormously larger predators. The tremendous ecological success of aculeate Hymenoptera rests substantially on their possession of a sting apparatus and venom with which to defend against even the largest vertebrate predators. To determine the defensive effectiveness of hymenopterous venoms, venoms from nearly a hundred species in 40 genera from 9 families were collected and analyzed. Insect dry weight, venom dry weight per insect, venom lethality to mice, painfulness of stings to humans, and populations of adult individuals in colonies of social species were determined. In selected species, encounters with potential mammalian, lizard, or anurian predators were designed. The results revealed that solitary aculeate species rely on different venom properties for defense against vertebrate predators than social species, but that the venoms of both groups can be highly effective in deterring predation. Solitary species have venoms possessing very little ability to cause physiological or lethal damage to predators, instead relying mainly on the ability of the venom to induce intense pain in the stung victim. Pain alone acts primarily as a form of Batesian mimicry that warns the predator that the prey is "dangerous". Social species typically possess venoms that induce both pain and have lethal activity, a combination that induces damage in the stung target and reinforces that damage with pain. Overall, venoms appear to be the most universal and effective defenses of aculeate Hymenoptera against vertebrate predators and are the proximal cause of the evolution of sociality in Hymenoptera.

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**DEFENCE AGAINST MICROORGANISMS IN THE ANT
MYRMECIA GULOSA AND THE TERMITE *NASUTITERMES*
*EXITIOSUS***

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Many aspects of the biology of social insects, including colony organization, may be responses to selection for defence against pathogenic microorganisms. We have been investigating microbial control in the ant *Myrmecia gulosa* and the termite *Nasutitermes exitiosus*. In the ant, the metapleural glands produce secretions with strong antimicrobial activity against a variety of microorganisms including Gram positive and Gram negative bacteria and several fungi including *Candida albicans*. Chemical analysis of the secretions is in progress. There are several active fractions, none of which have been previously reported. Workers transferred to sterile vials upon leaving the nest have very few microorganisms on the integument. Remarkably, this surface is almost sterile. However, males and juveniles lack metapleural glands and, if sequestered from workers, quickly succumb to microbial proliferation and disease. Overall, the control of microorganisms in colonies of this ant is by the secretion of antimicrobial compounds by workers. In contrast, microbial control in the termite *Nasutitermes exitiosus* is, at least in part, the result of the construction of the nest mound. The outer layers have low concentrations of organic material and very low matric potential, both of which militate against microbial growth. Within the nursery, however, conditions suitable for the development of termite young also appear favourable for microbial growth. Experiments are in progress to determine whether or not antimicrobial substances are produced to defend this crucial part of the colony.

Mandibular gland secretions of leaf-cutting ants: role in defence against alien fungi

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Volatile chemicals produced in the mandibular glands of leaf-cutting ants of the genera *Atta* and *Acromyrmex* had significant inhibitory effects on the germination, growth and development of certain fungi in laboratory cultures. Marked qualitative and quantitative differences were observed between fungal species and the chemicals tested. Preliminary results with *Attamyces*, the symbiotic ant-fungus, showed a similar pattern of response in terms of sensitivity. However, clear cut halos were not observed possibly suggesting an attenuation effect. The strains of *Attamyces* cultured by leaf-cutting ant colonies may be subjected to selection pressure by the presence of volatile chemicals, this could lead to tolerance which laboratory strains have lost over time. Mandibular gland secretions are known to function as pheromones controlling alarm/defence behaviour. Their additional role as antifungal agents may be necessary for preventing the symbiotic fungus from being overrun by competing species.

PEST ANTS

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In the world's urban environment, ants are one of the most important household pests today. They cause annoyance and undue stress, can spread pathogens, and even be life-threatening with their stinging. Some pest ants can also damage crops and agricultural equipment, wood, electrical equipment, communications and computer equipment, roofs, roadways and foundations, injure domestic animals and wildlife, and reduce biodiversity (see Vander Meer et al, 1990; Williams, 1994). Fortunately, only a tiny number of ants cause problems with the majority belonging to the genera Camponotus, Linepithema (= Iridomyrmex), Monomorium, Paratrechina, Pheidole, Solenopsis, Tapinoma, Tetramorium, Acromyrmex, Atta and Wasmannia. This symposium will address several species of pest ants including topics on their biology, behavior and the latest techniques on their control.

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BIOLOGY AND BEHAVIOUR OF *MONOMORIUM PHARAONIS* (L.) IN RELATION TO OPTIMISING CONTROL STRATEGIES IN PUBLIC BUILDINGS.

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Ants are communal insects that live in complex social groups based on a co-ordinating centre of colony life - the nest. Many aspects of the behavioural and physiological biology of pest ants predispose them to certain insect pest control strategies. This paper discusses the way in which a thorough understanding of the biology and behaviour of the pest ant *Monomorium pharaonis* has been used to improve the success of the techniques used to eliminate this species from houses and other public buildings. In addition, those instances where the biology of this species renders it less susceptible to certain techniques will be explored, as will the impact of some future pest control technologies that may be employed against infestations of *M. pharaonis*.

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PEST ANTS IN THE U.S. AND SOUTH AMERICA: AN OVERVIEW

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In the year 2000, 40% of the world's population will be living in cities and more than 80% of the population growth during this time will occur in urban areas. Thus, the impact of household insects on humans in the urban environment will be even greater than it is today. A recent study in the United States indicated that the most important household nuisance insect pests were ants. There are more than 20 species of ants that will cause some problems in the United States and South America. The majority of pest ants belong to the genera Camponotus, Linepithema[=Iridomyrmex], Monomorium, Paratrechina, Pheidole, Solenopsis, Tapinoma, Tetramorium, Acromyrmex, Atta, and Wasmannia. They can annoy and cause undue stress and cause disease by spreading pathogens, and can be life-threatening when hypersensitive individuals are stung. Pest ants can also damage crops and agricultural equipment, wood, electrical equipment, communications and computer equipment, roofs, roadways and foundations, injure domestic animals and wildlife, and reduce biodiversity. The habits of most pest ants make control techniques utilizing sprays and dusts ineffective because these treatments kill foraging workers but do not result in the elimination of colonies. Toxic baits are the method of choice for controlling pest ants. Research efforts are underway that will lead to the development of a holistic approach utilizing more effective, and environmentally safe methods for the control and management of pest ants.

ANT SUCCESSION IN FORESTS AND SAVANNA IN TROPICAL SOUTH AMERICA

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Clearings in primary forests in the Orinoco basin produce locally a large decrease in plant cover and plant species richness. The clearing however does not affect the ant species richness in those patches. Nevertheless, the forest never seems to recover to its initial species composition as indicated by ant and plant species composition. Ant species composition varies greatly during the recovery of the forest as measured during periods of up to 45 years after clearing. Species which dominate until 20 years after clearing the forest patches include *Wasmania auropunctata*, *Tapinoma*, *Paratechina*, and *Pheidole* spp. Once these species dominate in the patch, they seem to affect the ant community in such a way as to affect the recovery of the insect fauna irreversibly, impeding the re-establishment of the original forest ecosystem and thus orienting the development of new types of forests. Thus, the forest ecosystem seems to suffer from invading colonizing species in ways comparable to ecosystems suffering invasions of exotic ants.

STATE OF THE ART ON ALTERNATIVES TO CHEMICAL CONTROL OF LEAF-CUTTING ANTS IN BRASIL

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Current leaf-cutting ant control in Brazil has been mostly conducted by means of chemical products in granulated baits. At present, the number of available active ingredients is quite reduced. These are sulfluramid and diflubenzuron. Other methods as well as IPM strategies for leaf-cutting ant control are under investigation. For instance, *Eucalyptus* resistance studies have indicated that some species could be recommended for planting in programmes of reforestation. Different plant groups have been studied for toxicity and repellency to leaf-cutting ants with some promising results, although in a pioneer stage. Studies on pheromone use to enhance bait attractiveness are still being conducted, however, have not been successful so far. Expectation on the utilization of natural enemies, especially fungus has motivated some projects on biological control. Up to now, these have been applied in the field yet. Research on juvenile hormones were discontinued due to their poor performance. Therefore, a lot of effort still has to be put in order to achieve some degree of success.

CONTAINERIZED ANT BAITES USED IN A PERIMETER TREATMENT STRATEGY CAN CONTROL ARGENTINE ANTS

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Two commercial containerized ant baits containing either sulfuramid or hydramethylnon were evaluated in a perimeter treatment strategy for the suppression of Argentine ant, *Linepithema humile* (Mayr), populations at an apartment complex in three temporally separated trials. Baits were placed at 3-m intervals around the outside perimeter of 20 buildings and replaced at 2 to 5 week intervals. Ant numbers were monitored outside each test building at least once a week using 50% honey water. Bait acceptance by Argentine ants as indicated by the percent of empty bait stations retrieved ranged from 50% to 95%. Buildings receiving baits provided the same or reduced numbers of ants following treatment. In contrast, the control building showed a greater than 4-fold increase in the numbers of ants during the same time period. Bait acceptance and effect of toxic bait consumption on the foraging activity of field colonies also were assessed. Nine individual colonies were randomly assigned to receive one of three treatments: one of two containerized baits or an untreated control. Ant foraging activity was measured using honey-water monitoring stations placed at 0, 1, and 3 m from the colony nest-site. Both containerized baits reduced ant foraging activity to zero ants per monitor within 6 wks, if the equivalent of one containerized bait station was consumed by the colony.

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THE IMPACT OF THE MICROSPORIDIAN DISEASE,
THELOHANIA SOLENOPSAE, ON FIELD POPULATIONS OF
SOLENOPSIS RICHTERI IN ARGENTINA.

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The impact of the microsporidian disease, *Thelohania solenopsae*, was evaluated in field colonies of the fire ant *Solenopsis richteri*. The presence and abundance of each fire ant caste and the myrmecophiles with the colony were examined. The size of infected colonies were substantially smaller (67%) than healthy colonies. The number of colonies per hectare also declined as the presence of disease increased. Polygyny was found in 41.5% of infected colonies and 25.7% of healthy colonies and the mean number of queens per colony was 4.6 and 7.2 respectively. Worker brood, adult females and males were as frequent in infected as in healthy colonies. However, sexual brood was less frequent in infected than in healthy colonies (17% vs. 37%) and there was a 4 month delay in the production of adult males in the infected colonies versus the healthy ones. The presence of myrmecophiles was as frequent in infected as in healthy colonies, but the bug *Blissus parasigaster* was more abundant in infected colonies. *T. solenopsae* appeared to be an important growth limiting factor of field colonies of *S. richteri* in Argentina.

PEST ANTS IN EUROPE: AN OVERVIEW

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Among the nearly 560 species of ants recorded in Europe (from France to Black Sea) about 40 (7%) are recognized as introduced species (Agosti, 1989). The great majority of pest ants

Subfamilies of Formicidae in Europe	Number of species	Number of introduced species	Percentage (%)
Ponerinae	18	5	27
Leptanillinae	2	-	-
Dorylinae	2	-	-
Myrmicinae	343	17	5,0
Dolichoderinae	25	3	12,0
Formicinae	165	13	7,9
Total	555	38	6,8

in Europe belong to the group of introduced species included in the following genera: Linepithema (= Iridomyrmex), Monomorium, Tapinoma, Tetramorium and Pheidole. Some of these pest ants species have already a long story in Europe, like Monomorium pharaonis (England 1837) or Linepithema humile (Southern France 1904-1905). Others have been discovered later like Pheidole megacephala, or Paratrechina longicornis (see Bernard, 1968). Recently a new pest, belonging to the genus Plagiolepis, was found in 1989 in a swiss tropical butterfly garden (later also in some greenhouses in the Netherlands). This undescribed species exhibits all characteristics of tramp species as defined by Passera (1994). Research efforts were made on biological aspects of this species (C. Bijleveld, unpublished) in order to develop an effective control of the population.

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THE DYNAMICS OF EXPLORATORY RECRUITMENT IN THE PEST ANT *MONOMORIUM PHARAONIS*: EXPERIMENTS AND MODEL.

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One aspect of the foraging behaviour of pest ant species that has rarely been addressed is their exploratory behaviour and the strategy they use to occupy novel areas. This information could be essential in understanding their ability to colonise new sites. In order to fill this gap, we investigated the exploratory behaviour of *M. pharaonis* workers when they encountered a novel area devoid of food sources, both at the individual and collective level. At the individual level, we show that, when progressing on unmarked area, whether moving out from the nest or in its direction, ants lay scent marks on the ground more or less continuously. These scent marks act as a system of chemical mass-recruitment that induces other workers to rush out of the nest and disperse over the novel area. This effect is more pronounced with a starved than with a fed colony. The exponential build-up of ants observed on the area can be described by a mathematical model based on a logistic growth equation. After 30 to 60 minutes, depending on the size of the colony, a network of exploratory trails diverging from the entrance of the nest begins to emerge. In the absence of food sources on the area, this network remains stable over a period of several days. The chemical scent-marks left by exploratory workers do not deter workers of conspecific colonies from entering the area and may thus act more as a "home-range" marking rather than as a territorial pheromone, *sensu stricto*. The exploratory recruitment and the formation of exploratory trunk-trails allow *M. pharaonis* to rapidly occupy a novel area, to pre-empt potential competitors and promptly mobilise workers for the defence of food sources. A similar exploratory strategy appears to be used by other pest ant species such as *Iridomyrmex humilis* or *Wassmania auropunctata* and could explain their success in invading new niches and displacing other ant communities.

OUTBREEDING IN THE ARGENTINE ANT *LINEPITHEMA HUMILE* AND GENE FLOW PERFORMED BY THE MALES

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Inbreeding might have important consequences for the genetic structure of insect societies. In the Argentine ant *Linepithema humile* = *Iridomyrmex humilis*, as in some other ant species, mating occurs in the nest and new colonies are formed through budding. Intranidal mating has frequently been assumed to lead to inbreeding in ants. However, genetic studies detected no significant level of inbreeding in the Argentine ant. Furthermore, the relatedness among nestmates was not significantly different from zero, suggesting that gene flow occurs among colonies. In contrast to females, males disperse on the wing and they might be an important source of gene flow among colonies. In this study we investigate whether dispersing males can enter foreign colonies, and if so, whether they can mate with resident virgin queens. We also tested if the propensity of males to disperse is affected by the expectation of mating in their mother nest. Field experiments showed that males were accepted into foreign colonies only when these colonies contained female sexuals, or queen pupae. Before and after the time of production of female sexuals, workers attacked and killed most of the foreign males. Laboratory experiments showed that males that successfully enter foreign colonies can mate with resident female sexuals. The propensity of males to disperse was significantly influenced by the presence of female sexuals in their nest. Males were more likely to fly out from colonies containing no females sexuals than from those with them. This behaviour could mediate gene flow between colonies and account for the lack of significant inbreeding in this species.

CARPENTER ANT BIOLOGY AND ITS SIGNIFICANCE IN CONTROL

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In the U.S., current methods of carpenter ant control are time-consuming, labor-intensive, and, hence, problematic. Investigations into nutritional ecology and behavioral physiology provide information directly exploitable toward the development and optimization of toxic baits against carpenter ants, which could greatly enhance the efficiency and reliability of treatment. Minimum size threshold for the passage of food particles through the proventriculus has been determined using carpenter ant workers. This threshold lies in the nanometer range, smaller than the present lower size limits of insecticide microencapsulation. Food preference was examined under natural conditions and controlled experimental conditions. Under natural conditions, macronutrient collection by arboreal carpenter ant nests was quantified through gut content analysis. On a per weight basis, ten-fold more carbohydrate than protein was collected by foragers. In addition, protein collection was clearly bimodal. Under experimental conditions, weight of food removed from the test area was used to measure macronutrient collection by foragers. On a per weight basis, a maximum of 20% of carbohydrates provided were removed, while protein represented at least 80% of food removed. Such results suggest that protein may be the limiting nutritional resource under natural conditions. Lipids represented a very minor dietary constituent in both studies during the entire active cycle, although quantification of energetic reserves of overwintering workers showed that lipids were the primary energetic reserve during overwintering.

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SOCIALITY IN OTHER ARTHROPODS:

INTRODUCTION

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Notable discoveries concerning the evolution of sociality in animals other than so-far-known eusocial animals, the Isoptera, Hymenoptera, aphids and naked mole-rat, have been reported during only four years since 1990, when the last international congress of IUSSI was held in Bangalore, India. These are discoveries of eusociality in thrips (Crespi, 1992), ambrosia beetle ((Kent and Simpson, 1992), and Damaraland mole-rat (Jarvis et al., 1994). Experimental demonstration of defensive role of aphid soldiers, discovery of subsociality in mites and development of studies on subsociality in spiders and hemipteran and coleopteran insects can be added to the above list.

In this symposium, topics of the evolution of sub- and eusociality in spiders, mites, Isoptera, burying beetles, aphids and thrips will be presented. Aphids and thrips have soldiers but they don't have foraging workers. Studies on these groups may facilitate discussions on the evolution of soldier caste in termites. Thus general discussions in the proximate and ultimate causes of social evolution, in comparison with Isoptera and Hymenoptera are welcomed.

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SOCIAL EVOLUTION IN MITES

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Mites are small organisms having low mobility. Such a peculiarity may inevitably increase probability of kin interaction. If kin selection as defined by Hamilton (1964) is an important prime mover of social evolution in animals, we would be able to recognize many examples of sociality in the order Acari as well as other animals having similar peculiarity. However, evidence of social evolution in this order had been rather scarce at the time when Buskirk (1981) reviewed the Aracnida sociality. During the last decade, however, we have seen several fascinating examples of mite society. First, I intend to describe subsocialities observed in spider mites (Saito, 1986). Next I shall overview the cues of social organizations including parent-offspring inter-actions in the order Acari. A quick scanning of this order suggests that a kind of social organization is occasionally recognized in male-haploid and thelytokous species, but not in diplo-diploids. Although whether the factor of low mobility of mites or their haplo-diploidy is the cause of the observed pattern has not yet been determined, the kin selection appears to be one of the basic aspects explaining social evolution (Hamilton, 1972). I thus focus on the male-haploidy which makes closely related individuals able to interact. Furthermore, I will also address the possibility that the genetic system itself can explain the evolution of social life (Saito, 1994).

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EVOLUTION OF SOCIAL BEHAVIOUR IN BURYING BEETLES

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Beetles of the genus *Nicrophorus* are well-known for the elaborate parental care behaviours they exhibit on carcasses. Their unique behavioral adaptations apparently arise from special features of the larval food source. Small carcasses are protein-rich and allow rapid development, but they are also rare and hard to find. Beetles on carcasses often behave as if the present reproductive attempt was their only opportunity. Neither males nor females that lose intrasexual interactions over carcasses abandon the carcass once their role as a loser has been determined. Instead, they stay near the carcass for days to secure a small reproductive return. Loser females often lay a few eggs, while males typically mate a few times and sire about ten per cent of the brood. The only mechanism for recognizing their own larvae that burying beetles possess is a very inexact temporal one, such that the subdominant individuals' offspring are reared by the dominant pair. Multiple-female associations can be found on carcasses that are large for the species in question. In these instances, females often tolerate each other and occasionally even regurgitate to the larvae simultaneously; two males have also been found on large carcasses with broods at an advanced state of development, suggesting that males may also form associations in providing parental care. In most cases, however, one male and female or a female alone provide care for the larvae. The male's role in parental care is not fully understood, although the evidence available to date indicates that the main function of paternal care is defense of the carcass against conspecific intruders. However, males provide care even in low-density populations with negligible risks of a take-over by intruding beetles, suggesting that the prolonged male stay near the carcass may have additional, as of yet undetected, functions. On large carcasses, a sexual conflict arises when the male attempts to attract additional females by emitting a sex pheromone and is attacked by his mate. Two females produce a larger brood than one, allowing the male to sire more offspring, however, the resident female would suffer a loss in reproductive success should a second female be attracted, because of inter-brood competition.

**A MOLECULAR PHYLOGENETIC ANALYSIS OF SOLDIER
EVOLUTION IN THE APHID FAMILY HORMAPHIDIDAE**

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The aphid family Hormaphididae contains approximately 25 species that produce altruistic defensive larvae, termed soldiers, that defend the colony against predators. Soldiers are frequently morphologically specialized and reproductively sterile. To elucidate the historical pattern of soldier evolution and provide a framework for ecological studies of soldier evolution I have constructed a phylogeny of selected species focusing primarily on the tribe Cerataphidini which contains many soldier producing species. The phylogeny was constructed based on mtDNA sequence data from the Cytochrome Oxidase I and II gene regions. The phylogeny suggests that soldiers have evolved at least four separate times and been lost at least once in this family. In addition, the results support the hypothesis of Aoki and Kurosu that two morphologically distinct soldiers produced during different parts of the life cycle represent separate evolutionary events. This conclusion was supported by analysis of alternative hypotheses for soldier evolution on near-parsimonious trees.

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REVERSED REPRODUCTIVE SCHEDULE & FACTORS CONCERNING SOLDIER RATIO IN THE EUSOCIAL BAMBOO APHIDS, *PSEUDOREGMA* SPP.

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Bamboo aphids, *Pseudoregma bambucicola* and *P. koshunensis*, have two morphs in the first instar larvae: completely sterile soldiers and to-be-reproductive ('normal') larvae (Aoki and Miyazaki, 1978; Itô, 1989; Sakata and Itô, 1991). Rearing experiments showed that, in both species, a single mother can deposit both types of larvae, and in *P. koshunensis*, mothers first deposit normal larvae during a few days and then deposit several or tens of soldiers. This is completely reversal of reproductive schedule of other eusocial insects; their queens first produce workers and then produce reproductives. Field surveys showed that the principal factor concerning the soldier ratio of *P. bambucicola* was colony size. Field experiments showed that there was negative correlation (although not significant) between soldier ratio in colonies and survival rate of released larvae of a syrphid fly, *Eupeodes confrater*, suggesting the defensive role of soldiers. On the other hand, *E. confrater* adults tended to avoid oviposition near colonies with high soldier ratios.

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HABITATS, PARASITES AND SOCIAL EVOLUTION IN THRIPS AND OTHER INSECTS

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I review recent discoveries of social behavior in Australian Thysanoptera on *Acacia*. This remarkable group now includes five species with soldiers, three species with pleometrotic colony-founding, one species with cooperative defense, and one species which exhibits foraging in groups.

Consideration of the behavioral ecology of eusocial thrips, aphids, beetles, termites, and vertebrates leads to the hypothesis that two conditions, (1) food-shelter coincidence, and (2) the need and ability to defend against predators and parasites, are sufficient, although not necessary, for the evolution of eusociality in group-living animals. Reasons for this association between ecology and eusociality include extremely high value of the habitat, strong selection for defense, coevolution between attackers and defenders, possibilities for habitat inheritance, high relatedness in claustral situations, self-sufficiency of juveniles, greater ability of workers to reproduce, and trade-offs between defensive ability and dispersal.

This hypothesis predicts that new eusocial forms might usefully be sought among (1) bark and ambrosia beetles with substantial generation overlap between adults and offspring, (2) Psocoptera and Embiidina that inhabit large, long-lived webs, and (3) other insects that live within groups in galls.

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MATERNAL CARE AS THE PRECURSOR TO SOCIALITY IN CRAB SPIDERS.

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Maternal care is common to all social spiders, yet it is not well understood despite the potential effects of kin selection and/or maternal manipulation. Instead, sociality in spiders is most commonly explained by "altruistic" web building and foraging behaviour in aggregations at sites of high prey density. *Diaea* are crab spiders that do not weave a web, yet displays such social behaviours as loss of territoriality, cooperative prey capture, communal feeding and care of young. Field and lab experimental studies on two *Diaea* species show that mothers constructed larger nests of *Eucalyptus* leaves than juveniles alone which were more resistant to attack from avian predators, they were essential to the capture of large prey items on which the young relied, and that groups raised without mothers were more heterogeneous in size than those groups with mothers. Furthermore, groups that were more heterogeneous in size, and groups of unrelated individuals, became cannibalistic more rapidly during periods of food stress, wove smaller nests, and were more likely to emigrate individually from their nests. It is concluded that group living appears to be a consequence of subsocial maternal care, rather than foraging opportunities.

DO SOCIAL SPIDERS HAVE DIVISION OF LABOUR? A STUDY OF *ACHAEARANEA WAU* (THERIDIIDAE) AND SOME THEORETICAL CONSIDERATIONS

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Social spiders build communal nests and prey-capture webs, share food, and have communal care of the offspring (Buskirk 1981). The morphologically distinct castes characteristic of many eusocial insects are absent in the social spiders. This study examines whether there exist asymmetries in the performance of non-reproductive tasks in colonies of the New Guinea social spider *Achaeearanea wau* (Theridiidae). Observations of marked individuals and of activities performed by different size classes of spiders during the colony life cycle demonstrate that (1) there is no clear division of labour among adult females and (2) juveniles add tasks to their repertoire of activities as they mature. The lack of a clear separation of tasks by different individuals in a colony raises the question: what constrains the evolution of division of labour in social spiders? Genetic constraints associated with inbreeding may explain the lack of both reproductive and non-reproductive division of labour (Roeloffs & Riechert 1988). Using reliability theory analysis (Herbers 1981) on foraging behaviours in *A. wau*, I show that without division of labour, colony reliability increases asymptotically with group size. In *A. wau*, division of labor is not expected to improve the reliability of foraging for the colony.

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BEHAVIOURAL CHANGES DURING THE DEVELOPMENT AND MATURATION OF THE AUSTRALIAN SOCIAL SPIDER *PHRYGANOPORUS CANDIDUS*

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Phryganoporus candidus (= *Badumna candida*) is a periodic-social spider, i.e. it is tolerant, interattracted and cooperative in its juvenile but not its adult condition (Kullmann, 1968, 1972). This study investigated the behavioural changes that accompany the transition from the juvenile, social state to the subadult and adult phases which disperse and reproduce. At Townsville, North Queensland, *P. candidus* grows in sibling groups, together with the foundress parent, between March and October. Males do not mature and disperse until most or all females have dispersed (as subadults), despite the fact that males mature earlier than females when reared in isolation at constant temperature (Downes, 1993). The intraspecific interactions that parallel this pattern of maturation and dispersal were reflected in the behaviour of the spiders in laboratory trials: isolation prior to the trials produced or enhanced a decline in tolerance levels in subadult females and adult males, but not consistently in adult females, and not at all in subadult males. These differences, and perhaps also the apparent suppression of maturation of males in natural nests, suggest that pheromones may control or influence behaviour and/or development in this species.

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DISPERSION OF COLONIES AND RELATEDNESS IN
ANELOSIMUS EXIMUS

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Anelosimus eximius (Keyserling) (Araneae, Araneidae) is a social spider of south America. It inhabits the rain tropical forests where it colonizes the river edges and the road borders. This spider lives in large colonies (up to more than a thousand individuals in a single nest). From the literature and personal data three types of individual dispersal may exist, over short distances (less than 5 meters) by emigration of a part of the mother colony, over longer distances (up to 200 meters) by swarming of adult females and over long distances by passive emigration. The latter form may be the result of human activities or mammals. These different types of dispersal which may all occur in *Anelosimus eximius*, and reduced survival inside forest would result in higher relatedness among of individuals of colonies settled on the same road than which closer colonies but on other adjacent roads. In order to test relatedness between individuals, we used three different method; an ethological test and two biochemical methods to characterize the individuals of different colonie. For the behavioral test we put a stranger individual (of the same or of a different colony) in an homogeneous group of ten individuals of the same colony. We concluded that this individual, whatever its origin, is integrated in the group after a short period of time (24 hours). Biochemical studies (total enzyme and cuticular product analysis) showed that individuals of colonies along a road were more related than with individuals of colonies of adjacent roads. We conclude therefore, that the hypothesis of the action of the three types of dispersal could explain the distribution of *Anelosimus* along the roads. These predictions are confirmed by the survey during four years (1989 to 1992) of the colony distribution and development along different but adjacent roads in French Guiana.

POPULATION LEVEL CONSEQUENCES OF COOPERATION AND PERMANENT-SOCIALITY IN SPIDERS

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Social behavior involving cooperation among individuals that remain together throughout their lives while occupying a single communal nest has evolved independently at least eleven times among spiders (Avilés in press). Because mating takes place among nestmates generation after generation, this form of social behavior has resulted in highly subdivided population structures: populations which are collections of perpetually inbreeding colony lineages that give rise to daughter colonies or become extinct without mixing with one another. One of the consequences of such population structure is the possibility that selection may act on the colonies as units, leading to the female-biased sex ratios that characterize these species (Avilés 1993). Another, previously unrecognized, possibility is that the colony lineages, which grow in discrete steps and are subject to density dependence, may undergo chaotic fluctuations in size (e.g. May 1974). A mathematical model is presented that shows that cooperation and female-biased sex ratios, by increasing the net reproductive output of the colonies, should make such fluctuations more likely. Colony proliferation may have evolved as a response to overcrowding, but, because of the time lag in the development of the offspring and the impossibility of accurately predicting future levels of resources in a noisy environment, some colonies may nonetheless fail to proliferate and crash. The intriguing frequency with which social spider colonies go extinct (references in Avilés in press), may thus be partly driven by their own relatively large reproductive output. In a metapopulation, a high rate of extinction can be balanced by a high rate of proliferation, thus making species persistence possible; the resulting rate of colony turnover can become then a significant new factor in the subsequent evolution of the species.

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FROM SOLITARY SPIDERS TO SPIDER SOCIETIES

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Several hypothesis have been suggested to account for the origin and evolution of insect societies, with particular attention paid to Hymenopterans. These hypothesis however are difficult to generalize to other species of arthropods, such as spiders. Spider societies are rare, polymorph and polyphyletic. The transition from solitary to social life presumably occurred several times, independently within several phyla. It is thus unlikely that important changes in the species behavioral programme would have been required for sociality to emerge in spiders. According to our hypothesis, the single fundamental behavioral modification necessary for the transition from solitary to social life to occur would be the development of mutual tolerance among individuals, a behavioral trait initially present in all spider species. Other considerations show that tolerance is strongly dependent upon ecological factors, such as prey availability. One of the most striking feature of spider societies is the cooperation displayed by individuals in web building, parental care or prey capture, sometimes their transport. We suggest that these cooperative displays are the result of group life. Several characteristics of solitary species, comparable to social preadaptation, may have contributed to the emergence of these behaviors: interattraction and mutual tolerance among the young spiders, behavioral plasticity and web-mediated communication. In addition, the maintenance of spiders social structures should have been facilitated by the consequences of these cooperative behaviors: a larger range of prey species captured, an increased efficiency in the predatory behavior, the fast restructuring of the web, and the protection and feeding of the young.

**BEHAVIOURAL AND NEUROPHYSIOLOGICAL ASPECTS OF
INDIVIDUAL AND COLONY RECOGNITION**

Workshop organized by D. Brückner

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This workshop will bring together scientists working on social Hymenoptera to discuss the recognition behaviour of individuals and colonies within the different species. The topics of the talks will cover the neuroanatomy of the olfactory system and the underlying learning mechanisms. Recognition behaviour will be discussed in detail for ants, wasps and bees. The chemical signals used by the individuals in the recognition process will be presented at the latest level of scientific research. A final discussion will help to clarify the concept of individual, kin and colony recognition under the various scientific approaches.

ENCODING AND DECODING OF RECOGNITION SIGNATURES: AN INFORMATION PROCESSING OVERVIEW

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In social insects, chemical signaling is an extremely important channel for transmitting information that cues behavior in various kin, caste, intra- and inter-specific contexts (Getz, 1991; Smith and Getz, 1994). A systems approach to thinking about this information channel provides an excellent framework for identifying what the critical elements might be in each of the contexts mentioned above (Getz and Page, 1991), as well as where our knowledge might be lacking if we are to obtain an integrated information processing overview of chemical recognition systems in social insects. First I will identify and discuss essential aspects of the major elements of the process: chemical encoding of a recognition signature by the transmitting organism; passive or active broadcasting of the signature as a chemical signal; transmission of the signal; reception of the signal by sensilla on the antennae of the receiving organism; transduction and filtering properties of peripheral olfactory receptor neurons and integration of their response to obtain a representation with stable spatio-temporal characteristics; associative memory processing of this representation in both learning and cognitive phases; translation of innate and associate meanings into behavioral actions. Then I will briefly outline what we know about these elements in the honeybee (Getz and Akers, 1993) and some other social insects, and raise some questions relating to evolutionary links and constraints between these elements. Details of some of these elements in the context of specific organisms will be given by other speakers in the workshop.

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LEARNING OF ODOURS: THE BASIS OF INDIVIDUAL AND COLONY RECOGNITION

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Studies of odor recognition processes in social insects have focused on identification of odor cues and on how those odors come to be associated with nestmates. Odor cues can be produced by the insects themselves and/or derived from the environment, and covariation in amounts of individual odorants in mixtures can arise due to factors such as source as well as genotype (Smith & Breed 1994). Much less attention has been paid to the process of association of odors with nestmates. In most cases studied to date, nestmate odors must first be learned (e.g. phenotype matching) rather than acted upon through an innate recognition allele system (Smith & Breed 1994). Yet, beyond demonstrating that experience with an odor can modify responses to it, no study has investigated in detail the learning mechanisms involved. The exact nature to the learning mechanism (e.g., non-associative, associative, imprinting), how long the memory persists, and how accurate the memory remains over time all can dramatically affect the adaptive interpretation of the phenotype matching process (Smith 1993). One additional problem in learning theory, that of how learned information is translated in to behavior, is also applicable to recognition studies. Factors such as the context of recognition (e.g., mating versus nest defense) and physiological state of the interacting insects can affect what behaviors are elicited by a learned odor (Reeve 1989). All of these processes can have important effects on the evolution of the diversity of recognition cues (Ratineks 1991). Studies of individual, kin and colony recognition must now begin to focus on these latter processes.

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KIN AND NESTMATE RECOGNITION IN BEES

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Kin recognition within honeybee colonies could take place in the contexts of discrimination among queen larvae or discrimination among adult workers. A review of the available data shows that neither of these hypotheses has been adequately tested. New data, using color differences among bees in open-mated colonies, shows that cues are available which can be used in making within-colony discriminations among adult workers. These data support the hypothesis that cues are present that can be used to mediate preferential behavioral among super-sisters in open-mated colonies, but further experiments will be required to determine if such discrimination actually takes place.

Nestmate recognition in honeybees is mediated primarily by cues from the comb wax of the nest. The chemical composition of comb wax varies significantly among colonies. Bees are able to discriminate among combs from different colonies, but discrimination tests show that combs from genetically related colonies are more similar than combs from genetically unrelated colonies. A survey of compounds found in wax shows that alkanes, acids and esters may all serve as recognition cues, but tests of wax fractions indicates that the acid fractions have the greatest amount of recognition cue activity.

Within and between colony discrimination in honey bees rely on two apparently independent recognition systems. The cues used in within-colony kin recognition are under genetic control, but their chemical nature is unknown. More progress has been made on the chemistry of between-colony discrimination. Future work will focus on how the sensory information is integrated in making these discriminations.

Neuroanatomical Basis of Olfaction in the Honeybee

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The olfactory system of the honeybee is the best studied olfactory system in hymenopterans. The olfactory systems are build similiary in all insects. The antennal sensory neurons project in the antennal lobe, the first olfactory neuropil. Projectionneurons connect the antennal lobe with the ipsilateral mushroom body and the lateral protocerebrum. It is thought that these three neuropils are the brain areas, which are involved in olfactory processing. It is not yet understood which kind of operations are performed in each of these neuropils. There is much evidence that olfactory processing is not a simple sequence, where odour detection, component discrimination, mixture identification and memory are subsequent processing steps. In contrast to the investigations on other insect species, which often concentrate on the specialized system of sex-pheromone perception, research on the honeybee always dealt with the problem of a generalist system of odour perception. It is not known, if there are separate systems for (sex-) pheromone and other odour processing in honeybees at all. The same odour components can be found in flower blends as well as in pheromone blends (e.g. geraniol). On the other hand there seem to be no specialized olfactory sensory neurons in honeybees, as the so called queensubstance receptors are also sensitive to a variety of other odour components, too. There exists a dimorphism in the peripheral olfactory system of worker honeybees and drones. On the antenna of drones there are seven times more sensilla placodea (poreplates), which are the main olfactory sensilla. It is supposed that the increased number of the poreplates brings about an increased sensitivity for the queen pheromone. In the antennal lobes of drones there are 4 macroglomerular complexes. The fundamental question is, if the antennal lobe is build of seperate functional units (the glomeruli), which perform their operations independently of each other, or if the system is one complex network. We use an experimental set up, with which we selectively stain sensory neurones of individual sensilla placodea. Our experiments revealed that the sensory neurones of one poreplate project to different glomeruli and glomerular regions, which are widely distributed over the antennal lobe. Poreplates of the same flagellar segments do not project to similar or neighbouring glomeruli, rather the projection pattern is relativ in proportion to the AL-subregions.

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NEST MATE RECOGNITION OF WORKERS AND THEIR HYDROCARBON PROFILES IN JAPANESE, ASIAN AND EUROPEAN HONEYBEE.

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Very little is known about the chemical ecology of the Japanese honeybee, *Apis cerana Japonica* Rad. (*Acj*), which can share the same habitat with the European honeybee, *Apis mellifera* L. (*Am*), in Japan. Both workers were experimentally introduced to their own hive, to other nonspecific hives, and to hives of the other species as well. *Am* hives accepted 52% of the trials of day-0 *Am* workers and 85-88 % of the *Acj* foragers. On the other hand, *Acj* hives accepted almost all foragers from the other hive (96% average) and day-0 *Am* workers as well (90%). Hive mates as well as non-hive mates accidentally damaged during experiments were rejected, even in the case of the friendly *Acj*. As a result, nest mate recognition in *Acj* among different colonies and against different species was milder than that of *Am*.

Hydrocarbons (HC) were analyzed by GLC and GC/MS, and were compared among three species, using wax and body surface extracts derived from workers and drones. Each species was distinguishable not only by a combination of components, but also by occurrences of specific components. *Acj* workers contained C23 (16.7%), C25 (38.7%), and C27 (30.0%), and *Am* workers contained C25 (12.3%), C27 (25.2%), C29 (14.2%), C31 (16.4%), and C33 (18.3 %) with various degrees of unsaturation (0 to 3). Alka-6,9-dienes (C25 to C29) was present in *Acj*, while *Am* possessed dienes with (CH₂)_n (n > 3) between double bonds.

Hydrocarbon profiles among individual workers and drones of a hive were noticed to be different in *Acj*, *Am* in Japan and Asian bee (*Apis cerana indica*) in Nepal. Those from drones were divided into groups, of one or two, whereas those from workers were divided into groups of 3 to 10, depending possibly on the queen's multiple mating during her nuptial flight.

The hydrocarbon similarity index was compared among honeybee colonies of different locality and season. In *Acj*, the index was 52-78% in same area (*Am*:71%), 31-47% in different area, and 81-84% in different season.

In a few colonies, each drone had a very similar hydrocarbon profile. These results suggest that possibly there is inbreeding honeybee society and these drones are homozygotes.

THE POSTPHARYNGEAL GLAND DEVELOPMENT AND FUNCTION IN HYDROCARBON DYNAMICS IN *CATAGLYPHIS NIGER*

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The postpharyngeal gland is an ant specific organ occupying a large portion of the head with a lateral opening in the bottom of the buccal cavity. Its content consists mostly of hydrocarbons which were recently found to be congruent with those found on the cuticle. Ontogenetic studies on postpharyngeal gland ultrastructure and its chemical composition using electron microscopy and gas-chromatography revealed an elevation in hydrocarbon content that occurred with a parallel increase in the epithelial thickness of the glandular cells. The age dependent augmentation of the total amount of hydrocarbons was accompanied by a qualitative change in the relative intensity of the various components. The interrelationship between the postpharyngeal gland and cuticular hydrocarbons in individual ants was evaluated by an *in vivo* radiochemical assay while measuring *de novo* biosynthesis of hydrocarbons and their distribution in the body after injecting the ants with [¹⁴C] sodium acetate. In some of the ants, the possibility of an external transfer of hydrocarbons between the cuticle and the postpharyngeal gland was blocked by sealing the mouthparts. Adult ants were able to synthesize *de novo* hydrocarbons from acetate. This synthesis apparently takes place in tissues associated with the cuticle, since decapitated ants, i.e., deprived of their postpharyngeal gland, synthesized hydrocarbons in comparable amounts to normal ants. The results of time course experiments suggest that the newly synthesized hydrocarbons are sequestered by the postpharyngeal gland. In the absence of the gland (in decapitated ants) these hydrocarbons accumulated elsewhere in the body. Experiments using ants with sealed mouthparts further revealed that the hydrocarbons may reach the postpharyngeal gland both internally through the hemolymph and externally through the mouth during self grooming.

SPECIES-SPECIFIC RECOGNITION IN ARTIFICIAL ALLOSPECIFIC GROUPS OF ANTS

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The objective of this study was to investigate the role of early experience on the ontogeny of nestmate recognition and on long-term memory in ants. We analysed both the behavioural aspects and the cuticular hydrocarbons. Workers of two ant species, *Manica rubida* (Myrmicinae) and *Formica selysi* (Formicinae), were reared during 90 days in single-species groups or in mixed-species groups set up 5 hours after emergence. After this time, the mixed-species groups were split into two conspecific groups for 8, 15, 30, 60, 90 days, 6 months or 1 year. Ontogeny of recognition was evaluated before the separation between "unfamiliar" allospecific individuals proceeding from single- or mixed-species groups for periods of 5, 12, 24, 48, and 72 h and 8, 15, 30, 60, or 90 days after emergence. Long-term memory was evaluated after separation between allospecific individuals previously reared together ("familiar"), and between "unfamiliar" allospecific individuals from single- or mixed-species groups. The chemical results showed that: 1) in the course of the familiarization between species, individual hydrocarbon profiles gradually acquired some of the components characteristic of their allospecific nestmates; and 2) the amount of allospecific chemical cues carried by the individuals of both species decreased with the length of separation and only traces of allospecific hydrocarbons remained on *M. rubida* and *F. selysi* individuals after one year of separation. There were two important behavioural results: 1) Heterospecifically-reared individuals of both species gradually became tolerant for allospecific individuals from single-species groups. Moreover, conspecifically-reared individuals did not attack allospecific individuals reared in mixed-species groups. These experiments showed that allospecific recognition required the acquisition of a minimal quantity of allospecific cues. 2) After one year of separation, workers previously reared in mixed groups recognized familiar and even unfamiliar allospecific individuals. Although hydrocarbons are not generally considered to provide exclusive chemical basis for nestmate recognition, these results suggest that individuals recognized the allospecific cues borne by the partner, even when they were present in very small quantities and/or each individual learned allospecific recognition cues early in the imaginal life.

ROLE OF CUTICULAR LIPIDS IN NESTMATE RECOGNITION FOR SOCIAL WASPS

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Social wasps have a cuticular hydrocarbon composition which is species- and colony-specific. The paper of social wasp nests has a layer of hydrocarbons which also has a colony-specific composition. These hydrocarbons must be present on the nest for newly emerged wasps to recognize their nest and their nestmates. The following procedure was used during the summers of 1990-1994 in an effort to determine the role of these nest paper hydrocarbons in recognition. *Polistes metricus* workers were removed from their nests as pupae and isolated from adult wasps. Upon emergence, these workers were exposed to one of four nest conditions: 1) nests that were untreated; 2) nests which had their hydrocarbons extracted; 3) nests that had the hydrocarbons extracted and then had them reapplied; 4) no nest. After four days, the newly emerged wasps were observed for one hour in blind triplet tests for kin recognition with a nestmate and a non-nestmate. Only workers exposed to untreated nests and hydrocarbon-reapplied nests showed significant preference for their nestmates over the non-nestmates.

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NESTMATE RECOGNITION IN ANTS : PLASTICITY OF SIGNALS AND GENETIC FACTORS

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In the *Camponotus vagus* ant, the colony's chemical signature consists of some of the hydrocarbons which are present in the species-specific mixture but are the minor components of that mixture: the proportions of these hydrocarbons vary from one colony to another. Each category of individuals in a colony (i.e. those at various stages of development, those belonging to various castes) has its own signature, consisting mainly of the major components. This categorial signature furthermore varies depending on the individuals' physiological characteristics: among the workers' caste, those of the foragers and brood-tenders differ, and the queen's cuticular profile depends on her state of ovarian activity. These signatures are involved in the recognition processes on the basis of which the members of a colony behave appropriately depending on their partners' characteristics (Cf. Bonavita-Cougourdan and Clément, 1994).

The proportions of some cuticular hydrocarbons can also vary depending on the social environment. When *C. vagus* larvae are adopted by workers from another colony, their colony signature becomes similar to that of the adoptive colony, but their profile remains typical of larvae. In *Leptothorax lichtensteini*, the proportions of some of the cuticular hydrocarbons vary with the composition of the colony (Provost et al., 1993). The proportions of the hydrocarbons common to both the slave-makers *Polyergus* and their slaves, *Formica rufibarbis* or *cunicularia*, vary upon mutual exposure, in that those of the *Polyergus* adjust to those of their slaves, while the reverse process also occurs but to a lesser extent. Here each species however keeps its own cuticular characteristics. This tendency towards the homogenization of the cuticular profiles is consistent with the process of integration of the individuals within a social group.

The social environment may modify the effects of the genes involved in producing and regulating the colony signature, or that part of the signature which is common to two species (in the case of naturally mixed colonies), but it does not seem to affect the genes responsible for controlling the cuticular signatures labelling the stages of development and the castes.

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CUTICULAR HYDROCARBONS AND AGGRESSION IN COLONIES OF THE SLAVE-MAKING ANT *HARPAGOXENUS*

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Harpagoxenus sublaevis raid larvae of *Leptothorax acervorum* and/or *L. muscorum*, which after eclosion take care of the slave species. Profiles of cuticular hydrocarbons of the three species show strikingly low intraspecific variation for larvae. In colonies with only one slave species, the hydrocarbon profiles of the *Leptothorax* are species-specific and do not differ between unenslaved and enslaved colonies. Intraspecific variation is very low. The slave-making ant *Harpagoxenus* produces only minute amounts of own hydrocarbons and thus does not contribute to the profiles of *Leptothorax* workers. Instead, they show the same profiles as their hosts. In colonies with two *Leptothorax* slave species in approximately equal numbers, all three species show similar composite profiles with hydrocarbons from both *Leptothorax* species. In colonies in which one slave species clearly outnumbers the other, the resulting profile is dominated by the majority and may differ between heterospecific nestmate slaves. We observed aggressive interactions among slave-makers, between slave-makers and slaves, and among slaves in mixed colonies. The first two types of aggression appear to be correlated with reproductive competition for the production of males. Aggressive interactions among slaves, however, occur mainly between heterospecific slaves. In colonies, in which one slave species clearly outnumbers the other, the majority attacks and finally expels all nestmates belonging to the minority species. Our observations thus suggest that in *Harpagoxenus* colonies a homogeneous "colony odour" is not always achieved and that heterospecific slaves may occasionally be mistaken for alien ants.

REGULATION OF FORAGING SUCCESS BY DOMINANT SPECIES IN A DIVERSE ANT COMMUNITY OF THE AUSTRALIAN SEASONAL TROPICS.

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It is well known that the ability of social insects to monopolize rich resource patches represents one of the major benefits of insect sociality. However, this ability also has important implications for the dynamics of social insect communities: the foraging success of individual species is more likely to be influenced by competitive interactions with other species, than is the case in communities of solitary insects. This is particularly true for ants, the most abundant and aggressive of social insects, where competitively dominant species can largely determine the foraging strategies of other taxa. Here I describe an experiment which examines the effect of a dominant species on the foraging success of other species in a diverse (ca. 100 species) ant community in the Australian seasonal tropics. I ask the question: to what extent does the dominant species influence the relative foraging success of other species? The relative abundance of ant species at tuna baits was used to measure relative foraging success, and the abundance of the dominant species (the northern meat ant, *Iridomyrmex sanguineus*) was manipulated by fencing it out of experimental plots. Numbers of all other ants and ant species at baits in such plots were approximately double those in controls, and returned rapidly to control levels when fences were removed. Individual species differed markedly in their responses to the fencing treatment, indicating that meat ants had a major effect on the relative foraging success of other species. Species-specific foraging responses conformed to a general model of Australian ant communities, where taxa are classified into functional groups based largely on competitive interactions.

THE INFLUENCE OF ENERGETICS OF LOCOMOTION OF INDIVIDUAL ANTS ON THE FORAGING BEHAVIOUR OF DIFFERENT SPECIES.

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That social insects are able to use more complex foraging strategies than those available to solitary insects is aptly demonstrated in the ants where strategies range from individual foraging to the complex "army" ant type of group hunting. Ants use pedestrian locomotion for transport, thus the metabolic cost of locomotion of the individual foragers comprises a significant proportion of the total foraging energy budget. The assumption made in this study was that the type of foraging strategies available to ant species are constrained by the energetics of locomotion of the individual foragers. To compare the energy costs of foraging in several ant species the energy used per meter for locomotion by a representative ant of a colony when unladen and while engaged in foraging (defined as the unladen foraging coefficient by Bartholomew et al., 1988) was determined. The results indicate that there is an association between the foraging coefficient and type of strategy used. The ant species tested which use a more complex foraging strategy have lower individual costs of locomotion than solitary hunters. The energy cost of locomotion is, therefore, probably one of several factors playing a role in the evolution of foraging strategies.

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ENVIRONMENTAL EFFECTS ON FORAGING COSTS OF ANTS

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Current models of foraging behavior state that individuals should collect food in ways that maximize gain in relation to foraging costs. However, the actual costs of food collection, and therefore foraging decisions, are likely to vary considerably between environments. Ants provide a valuable system in which to examine how environment affects foraging costs and foraging strategy. All ants use terrestrial locomotion (walking) to gather food. However the ecological and physiological factors affecting foraging costs vary considerably among species. I measured energy costs for two ant species foraging in very different environments: the western harvester ant *Pogonomyrmex occidentalis* foraging in an arid grassland, and the giant tropical ant, *Paraponera clavata*, foraging in a rainforest. Energy costs of foraging for *Pogonomyrmex* were extremely small in relation to food gains; costs were approximately 1000 times lower than the reward of a single seed. In contrast, the cost of a single trip for *Paraponera* was approximately 30% of an average foraging reward. The differences in energy cost in relation to gain (the cost/benefit ratio) between these two species is as large as the range of variation in cost to benefit ratios for insects generally. Variation in foraging costs clearly affected foraging strategy. In both species, individuals used flexible foraging strategies to maximize colony intake. However, foraging decisions in *Pogonomyrmex* were relatively insensitive to energy costs. In contrast, *Paraponera* foragers varied recruitment and food collection strategies to minimize energy costs in relation to gain. Daily energy gains for *Paraponera* colonies closely matched energy requirements, suggesting that these colonies are extremely energy limited on a short term basis. In contrast, intake rates for *Pogonomyrmex* colonies are approximately fifty times daily energy requirements. It is likely that *Pogonomyrmex* colonies are not limited by immediate energy intake rates, as is often assumed by foraging models. Instead, they are more likely to be constrained by other variables, such as the ability to store food items without damage from fungus and other pathogens.

THE REGULATION OF WATER COLLECTION BY HONEY BEE COLONIES

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The water sector of a honey bee colony's economy involves a division of labor between the water collectors (foragers) who work outside the hive and the water consumers (nurse bees) who work inside. The nurse bees use water for evaporative cooling of the broodnest and for preparing liquid food for the larval brood. The nurse's rate of water consumption varies greatly, depending on the ambient temperature and the influx of nectar (which also provides water), hence a colony faces a problem of keeping its rates of water collection and consumption in balance. What tells the water collectors to continue or stop bringing home water? Our observations confirm an hypothesis proposed by Lindauer (1954): a water collector acquires information about her colony's need for water by noting one or more variables of her unloading experience each time she returns to the hive. The greater the need, the quicker she is able to start her unloading, the sooner she can end her unloading, the fewer encounters she has with hive bees refusing her water load, and the more bees she has unloading her simultaneously. Why does a water collector experience faster, easier unloadings when her colony's need for water is higher? It seems clear that the mechanism involves an increase in the number of bees accepting water, but it remains unclear how this comes about. We suggest two alternative hypotheses: (1) additional water receivers arise by nectar receivers switching to water reception when they sense a need for water, or (2) additional water receivers arise by nurse bees swinging into action (crawling to the unloading area and seeking foragers bearing water) when they need water in the broodnest. The second hypothesis seems more plausible because it invokes a direct link between water consumers and collectors. Experiments are planned for the summer of 1994 to determine which, if either, of these two hypotheses is correct. We will report our results in Paris.

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**ASYMMETRIES IN RECRUITMENT BEHAVIOR AND
RECRUITMENT RESPONSE IN THE ANT *FORMICA*
SCHAUFUSSI (FORMICIDAE)**

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Numerous studies have examined how the nutritional requirements of insect colonies are met by individual and collective foraging (Seeley et al 1991, Deneubourg & Goss 1989, Fourcassié & Traniello 1994). To examine how forager activity and recruitment behavior in *F. schaufussi* adjust to seasonal nutritional requirements and prey patch types, we measured the relationships between individual foraging behavior (area-related search behavior and recruitment [trail-laying] activity) and colony response (number of ants recruited) by offering foragers one of three patch types: persistent single load patches (single crop loads of 1M sucrose or a single termite), or persistent multiple loads (a 1cm diam. pool of 1M sucrose). Food items were offered 10 times at the same locality, before and after the mating flight. The foraging response of individuals was influenced by prey type only and was independent of load number, patch size and colony nutritional demands. Individual assessment of resource value (persistence and mass) did not seem to occur and colony response could not be predicted from trail-laying behavior. There were marked differences between the trail-laying behavior of individual ants and the recruitment response of the colony: individuals with very different frequencies of trail-laying across the ten rewards could induce very similar colony responses, while very different colony responses could arise from individuals with very similar trail-laying patterns. The lack of such a correlate may result from ecological factors constraining individual behavior.

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INTRA- AND INTERSPECIFIC VARIABILITY OF THE FORAGING SYSTEM IN *FORMICA* ANTS - DIFFERENT GENES OR DIFFERENT DEMOGRAPHIES?

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The moundbuilding *Formica* s.str. species show both intra-and interspecific variation with respect to the collective organization of foraging. It is often difficult to decide whether this variation reflects genetical adaptations or different outcomes of a single reaction norm. Proximate studies of the "social ontogeny" of the foraging system (seen as a "holistic", colony-level phenotype) may help elucidating this problem. The foraging systems of *Formica* s.str. species studied so far are based on the interaction between three basic processes: 1. social recruitment to food 2. the development of individually learned site allegiance (including individual or collective route or sector fidelity) and 3. a demographic parameter determining the quantitative proportion between spatially biased "veteran" foragers and still unbiased, recruit foragers. A system based on experienced foragers transmitting spatial traditions to novices appear geared to stable habitats. It can be shown, however, that depending on the relative contribution of each of the interacting processes, such systems may possess considerable colony-level flexibility and hence an ability to match even short-term changes in resource distribution. Seasonal, demographic cycles affecting the age composition of the worker population can be shown to modify the colony-level foraging pattern. Recent observations furthermore indicate, that the total size of the worker population has a qualitative impact on the overall foraging pattern, either directly (e.g. by influencing the threshold for massrecruitment), or, indirectly, through the correlation between colony size and the spatial scale of the foraging territory. These observations are supported by a theoretical model illustrating that the colony-level foraging pattern, especially the tendency to develop a system of permanent trunk routes, is, other things being equal, influenced by the scale of the foraging territory. The coupling between demographic parameters and the foraging pattern may represent a social reaction norm moulded by natural selection, although at the same time an example of "spontaneous order" based on self-organisation.

PRESENCE, SIZE, AND SPECIES OF RESIDENT SOCIAL WASPS (HYMENOPTERA: VESPIDAE) INFLUENCE RESOURCE CHOICE BY FORAGERS

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The role of visual cues provided by resident wasps on resource choice by yellowjacket and paper wasp foragers was investigated. Large spring queen yellowjackets and small early season yellowjacket foragers (*Vespula germanica*, *V. maculifrons*, and *V. vidua*) were collected, posed in lifelike foraging postures, and extracted in hexane to remove odors. These extracted wasps were then posed as though feeding at petri dish feeders bearing daisy-like flower models, equipped with microcapillary feeding tubes, and containing 3:1 honey:water solution. An array of five feeders was presented to foragers at a suburban and a woodland site in Saratoga Springs, New York. *Vespula germanica*, an introduced yellowjacket species that tends to dominate at rich resources, was the only wasp visiting the suburban feeders, preferentially fed on flowers with a posed wasp, fed most often next to large wasps, and showed no species specific landing preference. *Polistes fuscatus* foragers at the woodland site similarly preferred to feed on occupied flowers, and showed no species based foraging preference. *Vespula maculifrons*, *V. consobrina*, *V. flavopilosa* and *V. vidua* foragers exhibited resource choice patterns which included preference for unoccupied feeders, preferential feeding with a particular species, and lack of foraging preference. The presence, size and species specific markings of resident wasps influence resource choice by approaching social wasp foragers.

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MASS RECRUITMENT IN ANTS : AN AMBIGUOUS TERM COVERING DIFFERENT TECHNIQUES PARTLY CONSTRAINED BY BIOLOGICAL CHARACTERISTICS OF THE COLONIES.

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The various techniques of food recruitment observed in ants are often considered as different strategies that have been selected according to the environmental conditions in which the species live, such as spatio-temporal distribution, size and quality of food sources and competition (Hölldobler, 1978; Deneubourg et al., 1987; Traniello, 1989). It has also been suggested that foraging strategies could be related to colony sizes (Deneubourg et al., 1987; Pasteels et al., 1987). This hypothesis seems to be confirmed for individual foraging, tandem recruitment, group recruitment, and group hunting, but mass recruitment has been observed as well in small colonies as in middle sized and large ones (Beckers et al., 1989). In the present paper, we hypothesize that this poor relationship between the use of mass recruitment and the size of the colony is partly due to the ambiguity of the term mass recruitment. We think that a difference should be made between at least two types of mass recruitment. We suggest to call them "explosive mass recruitment" and "autocatalytic mass recruitment". We illustrate this point of view comparing the recruitment techniques of *Myrmica sabuleti* and of some other mass-recruiting species. *M. sabuleti* forms colonies of about one thousand workers and a few queens. Newly discovered large drops of sucrose solution or dead insects are exploited through an explosively increasing recruitment. This "explosive" recruitment is the result of the activity of only a few recruiters and allows *M. sabuleti* colonies to compete successfully with some other ant species, like *F. fusca*. This recruitment technique is very different from those of other mass-recruiting species, like *Solenopsis invicta*, *Lasius niger* or *Iridomyrmex humilis*. In those species, mass recruitment leads to a gradual increase of the worker population at the food source, as a result of the reinforcement of the trail over the course of time. This "autocatalytic" mass recruitment needs a great number of workers to function and should not be observed in species that have relatively small colonies. Available data support the idea that "explosive" recruitment is used by smaller societies. Species using "explosive" mass recruitment should rapidly colonize new food sources, but could be displaced later by species using "autocatalytic" mass recruitment. Observed competitions between *M. sabuleti* and *Lasius niger* support this view (De Vroey, 1979).

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RULES OF THUMB IN THE SOLITARY FORAGING STRATEGY OF THE ANT *PACHYCONDYLA APICALIS*. (HYMENOPTERA, FORMICIDAE, PONERINAE)

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The foragers of *Pachycondyla apicalis* hunt solitarily for food pieces which are more or less dispersed over a wide area: the foragers can, as a result, explore an area up to 30 meters from their nest. The collective hunting area is made up of a remarkable mosaic of individual zones where each forager is specialised: no interaction or chemical communication is used to coordinate this collective hunting activity. This is why we looked for the minimal rules of behaviour and for the decisions made by « naive » foragers in nature in the individual ontogeny of this task. The results showed that maturation (measured over an absolute time scale) does not play a role in the evolution of their performance as does the distance covered in foraging. The ontogeny can be explained, rather, by individual experience (measured over a relative time scale) which is accumulated through contact with the hunting area. It is, thus, on this basis that one approaches the study of individual mechanisms, beginning with three questions.

When to undertake a foraging trip? The interval between two foraging trips is reduced after the transportation of the first prey and then remains unchanged even after several consecutive successful trips. A single, unfruitful trip is sufficient to erase this effect and the period preceding the next outing approaches that of the period before the first prey was transported. Thus, each ant keeps, over the short-term, a memory of its earlier voyage which acts as a fixed rule.

When leaving the nest, which direction to take? Before the discovery of the first prey, the foragers tend to cover approximately the same zone where the earlier exploration was conducted. As soon as the first prey has been carried to the nest, the foragers strictly adopt the rule of returning to the last hunting site (following the same path and marking the same stops along that path): it is the same after the transportation of successive prey. This behaviour itself follows a fixed rule based on the ants' ability to revisualise the localisation of previous prey. After an unfruitful trip, the foragers keep the same direction corresponding to the last site, but their precise passage over the site itself changes progressively. The repetitive application of this fixed rule by all of the ants induces a sectoral specialisation.

Once on the previous hunting site, which direction to take? After the transportation of the first prey, the ant can choose any direction, but after the transportation of the second and third prey and with the accumulation of experience from successful trips, only the direction which distances the ant from the nest - often along the same axis - is increasingly favoured. This phenomenon is due to intracolony competition in the zone close to the nest which reduces the individual probability of a discovery, and, as a result of having distanced their prospection, the foragers attain regions where individual monopolies increase the probability of discovery. The application of conditional but fixed rules based on an individual evaluation of the density of prey is sufficient to generate the collective organisation as is confirmed by the model.

A LABOUR INTENSIVE FORAGING STRATEGY IN *MACROTERMES BELLICOSUS*, NEW KNOWLEDGE AND PROBLEMS

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Colonies of *Macrotermes bellicosus* are large mound-building and fungus-growing social organisms with a yearly food consumption of ≈ 125 kg (dwt) (1). The foraging area of a colony may extend over 200 to 2000 m² depending on the nest distribution density (2). Food allocation takes place exclusively from underground searching holes, which are found in densities of up to 300 per m². All food is manted with soil before foraged (2). This strategy implies high investment in both underground and aboveground building activity. High investment was also found from running activity on the underground exit roads of the mounds: 17 up to 32 kg (fwt) of termites (2.5. to 4.5 times the total termite biomass) circulate daily between the nest and the periphery. Av. 5700 returntrips (53g termites) are involved in bringing in 1g of food. To approach understanding of the ecological strategy based on such high investment into foraging, comparison with a related species *M.michaelseni* is indicated. *M.michaelseni* forages above-ground departing from scattered foraging holes and does not, except for large items, cover the food. It is therefore able to collect small and scattered food with less effort. Its network of underground galleries and foraging-holes is much less dense than in *M.bellicosus* (3). In *M. michaelseni* all building, exploration and foraging activity is performed mostly by the major worker caste, whereas in *M. bellicosus* building and exploration is economised by employing excessively minor workers. Only after food-detection the major workers are recruited (4). They are the specialists to gnaw off the foodmaterial. The major workers which in all *Macrotermes* are the genetic sterile males make out only 19% of the sterile population in *M.bellicosus*, an exception from the general sex ratio of near 1:1 in the genus (1). This reduction of a specialized caste is in agreement with the ergonomic optimisation model (5). In spite of caste ergonomy in *M.bellicosus* the kinetic effort around foraging remains considerable. This leads to the following working hypothesis: To gain the necessary amount of nitrogen from plant-litter a large excess of caloric engery is collected. This allows high energy investment in fungus-culture, in running and building activity with no extra food procurement. *M.bellicosus* on its emanzipated level of differentiation has made additional use of this energy compared to *M.subhyalinus* leading to the following ecological superiorities. 1. Better protection against predators by underground-foraging. 2. Foraging more independent on day-cycle due to the extended gallery-network and food-covering.

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FORAGING BEHAVIOUR OF THE HONEYBEE *APIS MELLIFERA* AND ENERGETIC EFFICIENCY OF THE HIVE

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The foraging behaviour of individual honeybees was recorded as determined by the flow ($\mu\text{l}/\text{min}$) of a 50% sucrose solution (w/w) provided by an artificial food source and by the distance (m) from this food source to the hive. On the *individual level*, the crop load (μl) attained in the foraging bout, the extent (min) of the pause between foraging bouts and the length (min) of the scenting activity with the pheromone of the Nasonof gland were recorded. On the *hive level*, trophallactic exchange behaviour between forager and hive mates and the number of new bees arriving at the food source as output of the recruiting process were measured in relation to the sucrose flow provided at the food source. In order to allow energy estimations, other parameters like pheromone scent marking of depleted feeders and metabolic rate during foraging were also taken into account. The adaptive significance of the results obtained are discussed in relation to the information channels used and to the economics of the foraging activity of the individual bee as an element of the hive.

INTRACOLONIAL CONFLICTS. 1. ULTIMATE FACTORS

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The dynamics of social groups are determined by a balance between cooperation and conflict among group members. In social insects colonies, the ever-expanding list of potential points of conflict includes the coexistence of multiple queens (polygyny), insemination of queens by multiple males (polyandry), replacement of deceased queens, usurpation of reigning queens, dominance hierarchies among queens and/or among laying workers, inequities in the contribution by different genotypes to the sexual brood (reproductive skew), and assorted disagreements on the source, size, and sex ratio of offspring. Our symposium will deal with the ultimate factors promoting these conflicts and those evolutionary factors underlying their resolution. Several talks will discuss the problem of reproductive competition in colonies containing several potential breeders. It will be shown that partitioning of reproduction among potential breeders is affected both by the genetical composition of the colonies and ecological factors that influence the opportunities for independent breeding and the benefits of cooperation. Another important issue that will be tackled in the symposium is the problem of sex ratio. Discussion will focus on the factors affecting the preferred sex ratio of workers. Several lines of evidence support the view that the workers, rather than the queens control sex ratios in the colonies, and that workers adjust the optimal sex ratio according to the genetic structure of their colony. Factors such as local mate competition and the presence of parasites and pathogens may also constrain how intracolony conflict is resolved. Some general features of intracolony conflicts emerge. First, the nature of the conflicts seem to be consistent across the taxa studied (including bees, wasps, ants, and Coleoptera). Second, the type of conflicts one observes in insect colonies depends primarily on the genetic composition of the colonies. Third, intracolony conflict generally incurs costs for members of the colony and in many cases mechanisms have evolved to decrease these costs. A common result is that the actual conflicts are frequently lower than the potential conflicts. This reduction typically is mediated by ecological factors that modulate the benefits of cooperation and the opportunities for independent breeding.

PARTITIONING OF REPRODUCTION AND ITS CONSEQUENCES IN INSECT SOCIETIES

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A critical feature of animal societies is the reproductive skew, a shorthand term for the distribution of direct reproduction among individuals in the society. In high-skew societies, actual direct reproduction is concentrated in one or a few dominant individuals in the colony ; in low-skew societies, reproduction is distributed more evenly among individuals.

Models of the evolution of reproductive skew have analyzed how ecological constraints on solitary founding, relatedness of potential breeders, relative fighting ability among breeders, and productivity advantages of peaceful association should influence the evolutionarily stable reproductive skew in insect societies. The general conclusions of these models are that the skew should increase (i.e., reproduction should become less equitable) as the relatedness between dominants and subordinates increases, the probability of successful solitary nest foundation by the subordinate decreases (i.e., for stronger ecological constraints), the subordinate's contribution to colony productivity increases, and the subordinate's relative fighting ability decreases. A further consequence of the skew models is that skews in matrifilial associations (asymmetrical relatednesses) will tend to be greater than those in semisocial associations (symmetrical relatednesses), even when breeders in each kind of association have the same relatedness to each other.

The degree of skew is predicted to influence other key attributes of societies, such as the frequency and intensity of dominance interactions and the division of labor within colonies. Thus, an understanding of the ultimate factors controlling reproductive skew may enhance our ability to explain and predict the occurrences of different kinds of societies in different ecological and genetic settings.

REPRODUCTIVE SKEW IN POLISTINE WASPS

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There has recently been increased theoretical interest in reproductive skew, the way in which reproduction is partitioned between the members of a social group. Modelling suggests that in social insects, relatedness and relative sizes of nest-mates are two important determinants in the evolution of skew, but as yet there are no data available to test these predictions. We have used DNA microsatellites and videoing of behaviour on the nest to directly measure both reproductive and behavioural skew in polistine wasp co-foundresses. We attempt to relate variation in skew to co-foundress relatedness, relative size and also co-foundress number, thus providing a test of the models.

DAUGHTERS KILL THEIR BABY SIBS AFTER CONFLICT OVER DOMINANCE WITH MOTHERS

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In primitively social bees guarding the nest is usually a well defined task, that may either be performed by the queen or by a worker. In the species with specialized guarding workers, these usually rank next to the queen in ovarian activity.

In the primitively social carpenter bee *Xylocopa pubescens*, guarding behaviour by a young female always preceded an attempt to take over dominance. These young females were usually the daughters of the dominant female, but also sisters and unrelated nestmates may guard and supersede. During a supersedure, severe fighting was observed. If the take-over is successful, one or more of the newly made brood cells may be opened, whereby the brood contents of these cells are destroyed. No influence of kinship upon the frequency of brood destruction by nestmates was found. However, superseding nestmates may benefit in terms of inclusive fitness by reallocating the pollen from newly made cells to their own brood, and by leaving intact brood that has finished the pollen supply.

By contrast, intruders that usurp a nest frequently, but not always, destroyed all brood cells present. They did not distinguish between different stages brood.

The differences in brood destruction pattern between nestmates and intruders may not be a consequence of kin selection, but of a differential knowledge of the position of the cells that contain pollen.

THE COSTS AND BENEFITS OF COMMUNAL BREEDING TO BURYING BEETLES

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Cooperation and conflict over reproduction lies at the heart of the evolution of sociality. Communal breeding, in which adults share a nest or a mate, is one path leading to complex social systems. Burying beetles (*Nicrophorus* sp) use small vertebrate carcasses as food for their young and can breed in pairs or communally. To understand the origin of communal breeding we must identify the options open to each individual and assess the relative success of each alternative. Reproductive success of females breeding in pairs and groups and the duration of care can be easily measured in this system. Now, with a PCR-based molecular technique (RAPD) to identify parentage, the relative reproductive success of communally breeding adults can also be measured. Communal breeding is much more common on larger carcasses than on smaller ones where the larger individuals of each sex drive off competitors. On a medium carcass, the reproductive success of the dominant female is reduced by 20% (range 0-50%) when she allows another female to remain. However, the diurnal species, *Nicrophorus tomentosus*, faces severe competition with flies when it breeds in August. When flies have oviposited on the carcass first, four communally-breeding adults rear significantly more young which offsets the loss to the dominant of sharing the resource. On larger carcasses, foursomes are even more successful than pairs and probably the share of the brood produced by the subordinate female is increased.

**SEX RATIO CONFLICT, QUEEN NUMBERS, RELATEDNESS,
AND SOCIALITY IN SWARM-FOUNDING WASPS**

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The swarm-founding epiponine wasps of the neotropics are characterized by high average queen numbers. This could lead to very low relatedness and the destabilization of sociality, particularly since workers are similar to queens and presumably reproductively competent. In fact relatedness is reasonably high, chiefly because queens are very highly related.¹ High queen relatedness arises from a colony cycle in which new queens are produced only on colonies with very few old queens (cyclical oligogyny).^{1,2} In *Parachartergus colobopterus*, reproductive swarming occurs during the wet season, as shown by seasonal peaks in both queen numbers and new nests, and an accompanying drop in average relatedness. New queens can also be produced without swarming; requeening events of this kind occur primarily in the dry season, perhaps when new queens are needed to keep the colony going. We tested the hypothesis that worker-queen conflict is the ultimate cause of cyclical oligogyny. Workers are predicted to favor female reproduction on colonies with few queens and male reproduction on colonies with more queens. This prediction was confirmed in all four species we studied.³ Paradoxically, though cyclical oligogyny seems to arise out of worker-queen conflict, it helps to maintain sociality by keeping relatedness high.

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ECOLOGICAL GENETICS OF QUEEN NUMBER IN MYRMICA PUNCTIVENTRIS: HOW MUCH ECOLOGY AND HOW MUCH GENETICS?

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Myrmica punctiventris, a cavity-dwelling forest ant, has populations with very different social structures at two sites in the Northeastern United States. Protein electrophoresis and behavioral tests have shown that a population of *M.punctiventris* in Vermont is strictly monogynous and goes through a cycle of seasonal polydomy: colonies fractionate into clusters of nearby nests in spring and summer, but recoallesce during the fall, into a single overwintering unit. In contrast, *M. punctiventris* is facultatively polygynous and does not exhibit seasonal polydomy in a population in New York. Relatedness between nest-mates matches Hamilton's expected values for the Vermont population, but is significantly lower than this expectation in the New York population. Within the New York population there is genetic differentiation between microhabitats. But allele frequencies overall are not different for the New York and the Vermont populations. A pilot experiment conducted by Herbers in Vermont showed that addition of food over two consecutive active seasons resulted in facultative polygyny, low nest-mate relatedness, and a breakdown of the seasonal cycle of polydomy, indicating that ecological factors can greatly alter social structure of this species. A further experiment in Vermont is fully exploring the effects of food and nest site availability on social structure of *M. punctiventris*.

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COOPERATION IN COLONIES OF THE LEAF-CUTTER ANT *ACROMYRMEX VERSICOLOR*

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Colonies of *A. versicolor* are frequently founded by multiple females. A division of labor occurs almost immediately upon colony foundation with a single foundress assuming most of the above-ground task associated with nest excavation. This same individual goes on to assume virtually all foraging for fungus garden substrate for the association. No evidence of behavioral dominance or coercion to assume this relatively risky role can be found. When workers eclose they do not treat the foundresses differentially, and secondary monogyny through queen conflict does not occur. DNA fingerprinting reveals that adult colonies in the field contain multiple females contributing to the reproductive progeny of the colony, suggesting that cooperation in these colonies is permanent.

PARASITISM AND INTRA-COLONIAL CONFLICT

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Polyandry and polygyny in social insects increase the genetic variability among workers of a colony. This tends to reduce the effects of kin selection and can potentially lead to increased intra-colony conflict over reproduction associated with negative effects on colony ergonomics. On the other hand, genetic diversity may increase colony viability for a number of reasons, including a decrease in the rate of within-nest transmission of pathogens. Such a pattern has been demonstrated with an intestinal trypanosome, *Crithidia bombi* and its host, *Bombus terrestris*. The advantage of polyandry in relation to parasite infections must depend on additional factors, however. Some theoretical results will be presented that analyse the advantages of polyandry in relation to parasite effects or mating costs. Furthermore, as experimental studies suggest, transmission of pathogens is affected by the age-dependent activities of the workers. Parasites could therefore play a subtle but important role in the colony organisation of social insects.

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INTRACOLONIAL CONFLICTS OF INTEREST IN A PRIMITIVELY SOCIAL BEE *LASIOGLOSSUM LAEVISSIMUM*

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Sweat bees have long been considered to be the best organisms with which to test hypotheses on the origin of eusocial behaviour. However, there have been no previous studies that have measured both relatedness among nestmates and the sex investment ratio for these bees.

I will present data on both of these crucial variables for the primitively eusocial species *Lasioglossum laevisissimum*, studied in Calgary, Alberta. This species is the most weakly eusocial insect for which these crucial sociobiological data have been obtained: it had an average of less than 3 workers per nest, one third of the workers were mated and almost two thirds of them had developed ovaries.

Relatedness was estimated from four polymorphic allozyme loci using the method of Queller and Goodnight (1989, Evolution 43:258-275). Relatedness values were high both among workers (0.76) and among gynes (0.74). whereas relatedness between workers and the gynes that they helped to rear was 0.64, significantly below the expected 0.75 value. Workers were significantly more closely and queens significantly less closely related to males than expected if nests were headed by one singly-mated oviposition-monopolising queen.

Detailed estimates of the investment ratio were obtained for the entire reproductive brood in each of 36 nests. The overall investment ratio was 2.2:1 in favour of females, indicative of worker control over the investment ratio. Furthermore, there was a positive correlation between investment in females and the relative relatedness ratio of workers to female versus male brood.

These data suggest that queens and replacement queens largely control oviposition but that workers control the investment ratio. The importance of indirect fitness benefits and haplodiploidy in the origin of eusociality in the Hymenoptera appears to be confirmed.

RESOURCE ALLOCATION AND WORKER-QUEEN CONFLICT IN *FORMICA TRUNCORUM*

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Hamilton's rule and the concept of inclusive fitness provide a theoretical basis for predicting reproductive characteristics of social insect colonies. Conversely resource- and sex allocation studies in social insects can be used to test inclusive fitness theory itself, since the optimal resource- or sex allocation ratios may differ for queens and workers depending on the degree of relatedness asymmetry within a colony. This study analyses predictions of ecological and genetical models for resource allocation both in the presence and absence of worker-queen conflict. In *Formica truncorum* both monogyne and polygyne colonies occur and each population tends to have only one type of colonies. In both population types on average 50% of the queens are multiply mated so the degree of relatedness asymmetry varies in monogyne populations, whereas it is invariably low in the polygyne populations. The impact of colony productivity, differential dispersal of sexes and relatedness asymmetry within colonies on resource allocation was analysed by measuring simultaneously both worker production, total sexual production and colony sex ratios. The genotype distributions of males and workers of monogyne colonies were used to assess queen mating frequency and the degree of relatedness asymmetry. The results show that genetic factors are the main determinants of resource- and sex allocation in the monogyne study population, whereas ecological factors best explain allocation patterns in the polygyne study population. In the monogyne population colony sex ratios were split in response to the degree of relatedness asymmetry of each colony, whereas local resource competition was the main determinant of sex allocation in the polygyne population.

SEX ALLOCATION, DISPERSAL DIMORPHISM, AND
REPRODUCTIVE EFFICIENCY IN THE ANT, *TECHNOMYRMEX*
ALBIPES

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In ants sex allocation is often female biased. There has been much discussion in evolutionary biology as to whether such female bias is caused by worker-control or local mate competition (LMC). On the other hand, it was pointed out that LMC can be discussed in the context of intrademic group selection. The dolichoderine ant, *Technomyrmex albipes*, has an unusual life cycle. There is a dispersal dimorphism in both sexes of this species. Alate sexuals disperse before mating, but wingless sexuals mate and reproduce in their natal colony. Colonies are founded by a single inseminated dealate queen. The foundress queen dies during the early stage of colony growth. Subsequently, supplementary reproductives - wingless males and females - which are all offspring of the foundress emerge from their pupae. After mating within the colony (inbreed), the wingless sexuals begin to reproduce. Mature colonies are extremely polydomous, polygynous, and often contain more than a million adults. Alates are produced in mature colonies seasonally, while wingless sexuals are produced throughout a year. Adoption of new inseminated dealate queens into established colonies does not occur. The average allocation ratio of alate sexuals was approximately 1:1, but that of wingless sexuals was extremely female biased (approx. 10:1; females:males). This is the first unambiguous special case in non-parasitic ants in which female bias is explained by the population structure that is, by LMC. The life cycle of *T. albipes* fits the intrademic group selection model of Wilson and Colwell. In fact, multiple regression analysis revealed that colonies with more female-biased sex ratio in parental wingless sexuals tended to produce more alate dispersers, and had a more brood (pupae) production per parent. These results support the discussions of the intrademic model.

PLANT-SOCIAL INSECTS RELATIONSHIPS

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Readers will find the outlines of a wide-ranging symposium set out in the following pages, covering the roles of social insects as predators, pollinators and mutualistic partners of plants, or else as mutualistic partners of fungi in the exploitation of living plants or the organic resources represented by their decaying remains. A degree of host-specificity is suggested, independently, in these relationships which implies a strong evolutionary interaction between plants and social insect taxa not generally noted for widespread herbivory or, as in the case of termites, assumed by virtue of their consumption of dead organic matter to be unaffected by the great variety of anti-herbivore defences deployed in the living plant.

The demonstration of such relationships implicitly underlines the role of social insects as superorganisms, with a real influence on the fitness of a range of plant types, at least in tropical forest ecosystems which the majority of papers address. The potential power of mutualistic relationships with social insects is amply illustrated by the parallel symbiosis of attine ants and Macrotermitinae, arguably creating the most virulent pests of arable crops known amongst social insects.

The theme of phylogeny runs through many of the presentation and readers will wish to note the wide range of techniques, including molecular methods, which can be employed to reconstruct the history of social insects-plants relationships. Though not explicit in any presentation, a study of ant-plants interactions lends support to foraging optimality theories which are proposed to account for the origins of eusociality in insects.

A NOVEL DEFENCE AGAINST LEAF-CUTTING ANT ATTACK IN THE PLANT *CALADIUM BICOLOR*

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The surface of mature nests of the leaf-cutting ant *Atta cephalotes* is normally kept free of vegetation, for reasons which are not understood. A survey of 12 such nests in Trinidad, showed that one of them carried a population of the Araceous plant *Caladium bicolor*, of a similar density to that found in the surrounding area. In an attempt to discover how this plant resisted the attacks of leaf-cutting ants, sap from the leaves was assayed for repellency to the ants, by adding it to a sucrose solution which they would normally drink. No repellency was found. The growth of the ant's mutualistic fungus was monitored on a glucose peptone agar medium, with and without added sap extract. The growth of the fungus was not inhibited by the plant extract. It was observed however that worker ants placed on the horizontal leaves of *C. bicolor* appeared unsteady, and fell off when they reached the edge. Laboratory experiments with captive ant colonies showed that although workers could traverse a horizontal section of leaf surface, none was able to climb it when the angle was increased to $>70^\circ$. Similarly, sections of petiole steeper than 50° could be climbed by only a small minority of workers. Brushing the leaf surface with a fine paint brush allowed the ants to climb 90° slopes with little difficulty. Scanning electron microscopy revealed that the leaf surface was covered with a layer of fine wax particles which were readily detached by light brushing. A more detailed field survey showed that some *C. bicolor* leaves on nest mounds had been cut by the ants, when the leaves were touching the ground or other objects. When small wooden access ladders were provided in the field, significant defoliation followed, which the free-standing control plants escaped. It is concluded that *C. bicolor* escapes defoliation by using the 'slippery pole effect', not only having a slippery petiole, but also a slippery lamina which prevent the ants from gaining access to their peltate leaves. When leaves touch other objects which the ants can climb, or when during dry spells the leaves wilt and touch the ground, they are vulnerable to defoliation. This defence against leaf-cutting ants is probably serendipitous, as *C. bicolor* is no more common on ant nests than it is away from them.

DEATH OF A NEST - THE BREAKDOWN OF THE MUTUALISM BETWEEN A LEAF-CUTTING ANT AND ITS FUNGUS

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Leaf-cutting ants have an obligate mutualism with a fungus which is found only in their nests. In dying colonies which have, for example, lost their queens, social organisation breaks down. This leads to a breakdown in the mutualism, which can be used to gain insights into how the ants culture their fungus. The symptoms of terminal nest decline in laboratory nests of *Atta sexdens* (L.) included both drastic changes in worker activities and in fungus garden appearance. Workers foraged less for leaves, but continued to tend their fungus gardens throughout the period of decline, signifying the importance of the fungus as a stimulus for them. In one dying nest, the presence of 'out of control' areas suggested that the ants usually 'prune' their fungus to keep it under control and to encourage the production of nutritive staphylae by the fungus. In such 'out of control' areas, this pruning has ceased. Further changes in worker behaviour were demonstrated by changes in infrabuccal pellet production. All solid material ingested by workers is trapped in the infrabuccal pocket and later egested as a solid infrabuccal pellet (Weber, 1972). Fewer infrabuccal pellets were produced in declining nests as workers became less active and the relative numbers of pellets containing plant debris decreased as workers ceased to forage. In contrast, pellets containing fungal material became relatively more common, because workers continued to tend their fungus garden.

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PLANT ALLOMONES AND IMPRINTING: TWO FACTORS THAT DETERMINE THE INSTALLATION OF DOMINANT ANTS IN TREE FOLIAGE

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We compared the distribution of two dominant, arboreal ants (census Leston 1973) on four types of plantation trees of different families. A global analysis of the results enables us to show that *Oecophylla longinoda* are found on citrus and mango trees whereas *Tetramorium aculeatum* are found on cacao and guava trees. But, on a smaller scale, these proportions can be inversed; we will see why.

Tests involving either winged females or workers with brood were undertaken in the laboratory. The ants were given the choice between two types of shelter made of the leaves of the four plants to be tested, compared two-by-two.

1st test: Ants originating from trees of families different from the ones to be tested. Statistics show that *O. longinoda* install themselves in shelters constructed from the leaves of mango or citrus trees rather than those made of the leaves of cacao or guava trees. The reverse is true for *T. aculeatum*. These results confirm those made based on an overall, ecological survey.

2nd test: Ants originating from one of the two tree species to be tested. Statistically, in all cases, the ants installed themselves in shelters made up of the leaves of the same tree species from which they were taken. There is, thus, a familiarisation which superimposes itself over a type of "spontaneous attraction" shown previously. This might explain the inverse proportions observed during the ecological survey at the local level. Among the ants bred in the laboratory, the nymphs, larvae, young adults or older adults were separated into four groups, each one being put into contact with one of the four tree species being studied. The testing of choice enables us to show that this contact was sufficient to condition the ants, if it took place during the larval or nymphal stages or at the beginning of the ant's adult life, but not later. There is, thus, a pre-imaginal stage of apprenticeship which is reinforced by a stage of precocious apprenticeship which predisposes the ants toward installing themselves in one tree species or another. The fact that there is a threshold after which one can no longer condition ants allows us to speak of a "type of imprinting".

MECHANICAL ASPECTS OF LEAF CUTTING AND THEIR EFFECTS ON BURDEN SIZE IN THE ANT *ATTA CEPHALOTES*

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The close correlation between the size of leaf-cutting ant foragers and the burdens they carry has prompted much speculation on the optimization of load delivery (Roces, 1990; Wetterer, 1991). The closer correlation of burden weight than area with forager size (Rudolph and Loudon, 1986) implies that the mechanism of load size determination is not a simple function of body geometry. In our study, leaf fragment weights were altered experimentally during the cutting process and the relationships between the total weights of severed fragments and the sizes of ants cutting them were compared. We then measured the shapes of fragments cut from laminar materials of variable thickness and compared the arc radii of cuts in different regions. Artificial alteration of fragment weights during cutting failed to influence the expected final weights of burdens, implying that the ants do not sense the weight prior to severance. Cutting ants were observed to change their stance when encountering regions of different thickness resulting in a significant reduction in the arc radius for thicker material. In consequence the burden weight represents a better correlate of worker size than fragment area. Load size appears to be determined by individuals as a response to the difficulty of cutting materials of different thickness.

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MICROTERMES AND PLANT ASSOCIATIONS

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A review of the food preferences of the major African crop damaging pest *Microtermes* spp. is given for different regions of Africa and elsewhere, together with the form of attack and factors affecting differences in plant susceptibility. Also examined is the possible relationship between resistance and indigenous origins.

ASSOCIATIONS OF *CLADOMYRMA* (HYMENOPTERA: FORMICIDAE: FORMICINAE) WITH PLANTS IN SE ASIA

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The Oriental plant-ant genus *Cladomyrma* inhabits several host plants of different families and orders, comprising trees and woody climbers in Peninsular Malaysia and Borneo. The colony founding queens chew holes into young plant internodes and hollow them out as nest cavities. Later, these initial nest chambers become enlarged by workers which excavate the twigs to provide shelter and substrate for brood and symbiotic Coccoidea (soft scales and mealybugs). In Pen. Malaysia the tree *Saraca thaipingensis* (Caesalpiniaceae) is regularly inhabited by *Cladomyrma petalae*. Other *Saraca* species (*S. declinata*, *S. indica*, *S. hulletti*) are not colonized by *Cladomyrma*. The host plant *S. thaipingensis* appears not to be a specialized ant-plant since it does not provide specialized structures for housing ants, such as swollen twigs or hollow stems with prostomata. However, it produces extrafloral nectaries on young leaves which attract many ants except *Cladomyrma*. Nevertheless, the activity of *C. petalae* workers on the plant surface is concentrated on young plant tissue. Preliminary data suggest a reduced herbivore damage level on young *Saraca* leaves patrolled by *Cladomyrma* workers. *C. petalae* was also found nesting in sympatric woody climbers *Strychnos vanprukii* (Loganiaceae) and *Spatholobus* sp. (Fabaceae). Whereas only a fraction of the *Strychnos* population is inhabited by this plant-ant, *Spatholobus* lianas were never found without *Cladomyrma*. At an early developmental stage young *Spatholobus* climbers produce conspicuous internodal swellings (myrmecodomatia) which provide large stem diameters necessary for colony founding queens. In Pen. Malaysia and Borneo the genus *Cladomyrma* is known to inhabit many more host plants: *Millettia nieuwenhuisii* (Fabaceae), *Crypteronia griffithii* (Crypteroniaceae) and *Neonauclea* spp. (at least 2 species; Rubiaceae). Recently, we found evidence that additional host plants do occur in Flacourtiaceae, Euphorbiaceae and Rutaceae. Since the genus *Cladomyrma* occupies so many unrelated plant species we assume that host-switching has occurred several times.

ANT-ATTRACTING PLANT STRUCTURES: FOOD BODIES OF SE ASIAN VITACEAE

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Food bodies are produced by a variety of tropical and subtropical plant species. They have long been hypothesized to attract ants and function as ant food although their collection has so far been directly observed only in a few plant species. Usually these are involved in highly specialized ant-plant associations where they perform an essential role in the maintenance of mutualisms. In contrast to another ant-related feature in ant-plant interactions - extrafloral nectaries - only little information exist on food bodies. Comparative investigations on their abundance, distribution and function are lacking. We have started studies on the occurrence of food bodies in the family Vitaceae in Malaysia. Here we compare 7 species: *Leea indica*, *Cayratia japonica*, *C. mollissima*, *Cissus repens*, *Tetrastigma pedunculare*, *T. lanceolarium* and *T. leucostaphylum* (all except *Leea* being climbers; second growth habitats are particularly prevalent). Food bodies were rarely found during field observations where insects continuously had access to the plants but were obvious on plants grown in the greenhouse or when ants were excluded. All species studied produced food bodies on the lower surface of the leaves. Additionally, food bodies were located on other plant parts (such as petioles of leaves, flowers and fruits, buds, tendrils, also on fruits). The species differed in number, size and also shape of their food bodies. Preliminary tests for glucose, protein and lipids indicated differences in nutrient contents and concentrations. Two species, in addition, provide sugary secretions from extrafloral nectaries as a complementary energy source. All 7 plant species were visited by a number of different ant species. The actual collection of food bodies was observed in several species (incl. *Crematogaster* spp., *Diacamma rugosum*, *Polyrachis* spp.). Presently we have started to take inventory of the herbivores and assess the possible protective role of the visiting ants (as was indicated in studies on non-mycorrhizal *Macaranga*-species providing food bodies).

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THE FIRST MYRMECOPHYTIC 2-PARTNER-SYSTEM IN THE GENUS *MACARANGA*: THE ASSOCIATION BETWEEN *MACARANGA PUNCTICULATA* AND A *CAMPONOTUS (COLOBOPSIS)* IN MALAYSIA

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In Peninsular Malaysia two myrmecophytic *Macaranga* species (Euphorbiaceae) exclusively occur in peat swamp forests : *Macaranga pruinosa* and *M. puncticulata*. *M. pruinosa* is associated with specific *Crematogaster* ants. Probably two similar *Crematogaster* species are involved, which can only be distinguished by morphometric characters of the queen ants. The ants feed on food bodies mainly provided on the stipules of the plants and in addition cultivate trophobiotic coccids in stem domatia. Thus, the association represents a three-partner-system. In the syntopic species *M. puncticulata*, we discovered a fully different myrmecophytic system. 65% of all *M. puncticulata* were inhabited by an as yet undescribed *Camponotus (Colobopsis)* of the *saundersi*-species group. Colonization of *M. puncticulata* was (contrary to *M. pruinosa*) restricted to shady forest sites. The high percentage of colonization as well as the mode of colony foundation indicate an obligatory association between the two species. Colonies are founded by queen ants which search for young host plants and chew entrance holes into the hollow stem domatia. The plants also provide food bodies and in addition offer nectar from glands situated along the whole leaf margin. In contrast to the so far investigated *Crematogaster* ants in *Macaranga*, *Colobopsis* sp. does not cultivate any trophobionts. This association is therefore the first record of a two-partner *Macaranga* myrmecophytic system. It also differs from *Macaranga-Crematogaster* in other characters e.g. large colonies may inhabit several neighbouring trees polydomously . The workers also collect insects as protein supplement, thus leaving their plants for foraging. Despite the differences, *Colobopsis* sp. fulfils the same protective role as already described for *Macaranga-Crematogaster*-associations.

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THE BIOLOGICAL INTERACTIONS BETWEEN ANTS AND CASHEW-TREE

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The biological interactions between cashew-tree/ants were studied envisaging future biologic control of pests and augmentation of productivity. The plants were distributed in twelve ranks of eleven plants each, individually marked from "A" to "L". Ten of each were randomly selected and isolated in the base, with a ring of grease. Nests of *Ectatomma quadridens* and *Odontomachus haematodus* were observed close to five of the isolated plants. The rest were destitute of terrestrial nests. Those were used as control plants, and only fifteen had nests in the surroundings. Eleven months afterwards was noticed that 67% the cashew-tree arthropods were ants, corresponding to 88% of the Hymenoptera. Amongst the most frequent ants became distinct : the arboreal ants *Dolichoderus (Hypoclinea)* sp. (26%), *Zacryptocerus* sp. (24%) and *Pseudomyrmex termitarius* (13%); the terrestrial ants *Ectatomma quadridens* and *Odontomachus haematodus* occurred in short proportion (3.3% and 3.4% respectively). The first species was a predator of the larvae of Cerambycidae (*Analeptes* sp., trunk perforator) and the adult of Coccidae and Membracidae. The former, a predator of nymphes of Membracidae, Psocoptera and small crickets. The analysis of vegetative conditions of the cashew-tree proved that non isolated plants presented 74% of the inflorescences, making evident the participation of the ants as agents in the development of buds, whether as predatory of pest of the cashew-tree or as pollinisateur.

THE PHYLOGENY OF THE FUNGUS-GROWING ANTS (MYRMICINAE: ATTINI) AND THEIR FUNGI

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Attine ants cultivate fungus gardens upon which they are obligately dependent for nourishment. Because no phylogeny for the tribe has been available, the evolutionary steps leading to this complex and remarkable behavior have remained obscure. Our goal in this study was to clarify the evolutionary history of the attine-fungus symbiosis by 1) determining whether or not the Attini are monophyletic; 2) identifying the sister group(s) of the Attini; 3) identifying the major lineages within the Attini; and 4) comparing the phylogeny of the Attini with that of their fungi.

We analyzed 44 morphological characters of prepupal larvae for 51 attine and 16 non-attine species, including 12 species previously proposed as sister groups of the Attini. The results strongly support the monophyly of the Attini. They further indicate that species of the genus *Myrmicocrypta* may retain many of the characters of the ancestral attine, and that the Neotropical *Blepharidatta brasiliensis* is the nearest non-fungus-growing relative of the Attini. Work carried out simultaneously with I. Chapela, U. Mueller, S. Rehner, G. Hinkle, and J. Wetterer focused on reconstructing the phylogeny of the attine fungi (all in the Basidiomycetes) utilizing morphological characters and sequence data from two different nuclear ribosomal DNA regions, and revealed that the fungal phylogeny is broadly congruent with that of the ants.

We conclude that the fungus-growing behavior has had a single evolutionary origin in the ants and that, within the Attini, mycelium cultivation is primitive and yeast cultivation is derived, contradicting the longstanding assumption that the yeast-growing *Cyphomyrmex* species are the most primitive Attini (Weber, 1958; Hölldobler and Wilson, 1990). Behavioral and ecological investigations into the origin of the fungus-growing behavior might most profitably focus on *Myrmicocrypta* and *Blepharidatta* species. The common ancestor of the monophyletic derived group containing the genera *Sericomyrmex*, *Trachymyrmex*, *Acromyrmex*, and *Atta* apparently "artificially selected" a strain of fungus that produces the food bodies known as "gongylidia," which are absent in the fungi of other attines. This evolutionary innovation may be partly responsible for the success of the leaf-cutting species.

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**PRODUCTION OF PSEUDO-POLLEN IN THE VINE TREE,
ACTINIDIA POLYGAMA, AS A STRATEGY TO ATTRACT
BUMBLEBEES**

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Fitness of entomophilus plants depend on the frequencies and duration of pollinators' visits. These factors are affected by the quality and quantity of reward offered by plants. I examined the relationship between the behavior of pollinators and the fitness of a vine tree which produces two types of flowers having no nectaries. Two bumblebee species, *Bombus diversus* and *B. sapporensis*, are the main pollinators of the vine tree, *Actinidia polygama* in Hokkaido, Northern Japan. *A. polygama* has androdioecious sex expression; a population consists of male individuals and hermaphroditic ones. Males produce normal pollen grains. On the other hand, the pollen grains of hermaphrodites are unfertile, containing about half as much protein as male pollen do. Hermaphrodites of this species, which bear no nectaries, seem to use such pseudo-pollen as reward or counterfeiter for pollinators. I controlled the number of anthers in male and hermaphrodite flowers at three levels and observed pollinating behavior of bumblebees. Bumblebees visited hermaphrodite flowers as frequently as male flowers, suggesting that they do not distinguish flowers with normal pollen from those with pseudo-pollen. They visited flowers with smaller number of anthers less frequently, and left earlier from flowers with fewer anthers. These results suggest that pseudo-pollen of hermaphrodite flowers effectively attract bumblebees. As accumulated settling time of bumblebees increased on each flower, the number of seeds increased with decreasing rate. Hermaphroditic flowers with fewer anthers produced fewer seeds. Thus, it is concluded that producing pseudo-pollen is a strategy for increasing the fitness of hermaphroditic individuals.

SOCIAL EVOLUTION IN INSECTS

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The evolution of social behavior is a subject of perennial interest, both within and outside the study of social insects themselves. In the past, social insects have been used as model organisms for ideas about sociality, serving to illustrate theories depicting animal societies as coherent "supraorganismic" units, as well as theories depicting them as dense aggrupations of competing individuals forced to cooperate by controlling matriarchs or the advantages of mutual aid. And, of course, they have served to examine the detailed predictions of kin selection theory. Social insects have also been used as extreme cases of intraspecific polymorphism and self-sacrificing aid, and to test more general ideas about evolution, as when Darwin emphasized the special difficulty for his theory to explain transgenerational inheritance of the specialized traits of sterile individuals. The study of social evolution in insects is now on the threshold of a new era in that "eusociality" (social life including sterile castes) has been discovered in several groups outside the Hymenoptera and the Isoptera, offering new opportunities to test old generalizations. In addition, a reawakening of interest in behavioral and developmental flexibility is beginning to add an ontogenetic dimension to general ideas about evolution. The lectures in this symposium exemplify these exciting new directions in research on social insects.

ALTERNATIVE PHENOTYPES AS THE BASIS FOR CASTE EVOLUTION

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Queen/worker dimorphism, a characteristic of higher sociality, is an often-cited polyphenism. The two castes differ morphologically, and these differences must be generated during the larval period in order to be expressed in the pupa or adult. One of the most profound effects of larval nutrition in insects in general is a plasticity in development affecting adult form. In simpler social systems, poor nutrition may reduce size and/or reserves. I argue that social Hymenoptera have incorporated reaction norms to larval food supplies into their social systems and these are consistent with patterns that would be advantageous in provisioning ancestors. Also, higher social lineages must have evolved from systems with such developmental, nutrition-based reaction norms, and these were canalized into discrete developmental switches. In social Hymenoptera, what factors favor the evolution of societies with polyphenic strategies, with discrete castes, over generalist strategies with only behavioral and physiological plasticity? Recent theory suggests that the population-wide accuracy of making 'correct' developmental choices is a critical factor. Accuracy is set by the availability and reliability of cues. Several types of cues, such as temperature and pheromones, are available to predict both non-social and social aspects of environment. In addition, polyphenism among workers has evolved in the ants. Reliable cues for predicting environment must also play an important role in the evolution of a work force that includes multiple forms.

THE EVOLUTION OF THE APHID SOLDIER MORPH

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Among aphids, soldier castes have been found in two families, Pemphigidae and Hormaphididae. The morphology and function of soldiers differ greatly from species to species. In *Colophina arma* Aoki (Pemphigidae), the soldiers have developed forelegs and shorter stylets than normal first instars, and counterattack insect predators with their stylets. On the other hand, the soldiers of *Pseudoregma* sp. (Hormaphididae) bear a pair of large horns on the heads and attack predators by stinging them with their horns. This study examined morphological variation in the soldiers and normal first instars of the two species and attempted to explain the origin of sterile soldiers. Morphometric analyses showed that in *Colophina arma* the regression slopes of several characters on the general size varied significantly between soldiers and normal larvae. By contrast, in *Pseudoregma* sp. morphological differences between soldiers and normal larvae were explained in several characters by a single allometry, suggesting that the morphological differentiation of the soldier caste from normal larvae occurred gradually with increasing body size. Although soldiers of *Colophina arma* have a distinct morphology from normal larvae, soldiers were morphologically similar to the first instars of the gall generation, which appear in the gall on another hostplant. Pemphigid aphids including *C. arma* are characterized by host alternation and polyphenism within the same clonal line. Among Pemphigids, mutants are known which erroneously bear a morphology that should appear in a different generation. Thus, it is hypothesized that the potentiality of producing alternative phenotypes within clones is responsible for the evolution of soldiers in *Colophina*. This hypothesis was tested by morphometric analyses.

ORIGIN AND EVOLUTION OF NONDISPERSIVE AND STERILE CASTES IN TERMITES

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Termites most probably derive from wood-dwelling roach-like ancestors living in familial groups, which evolved towards eusociality: all present-day termites possess specialized helper castes with low reproductive abilities, such as sterile soldiers or more or less sterile workers. Castes are determined epigenetically. I shall first address the question of the origin of such less or nonreproductive phenotypes. Previous hypotheses (Bartz 1979, Pamilo 1984) have emphasized the indirect fitness benefits helpers could obtain by behaving altruistically. However, observations of extant termite colonies revealed that individuals can be deprived of some direct fitness by the action of nestmates. For instance, in some species of the primitive family Kalotermitidae, an important number of nymphs have wing pads bitten off by other individuals. A simple model (Roisin 1994) shows that competition for resources allowing access to the alate flight is the most likely cause for the origin of such bites. Wing pad-mutilated nymphs are unable to proceed to the alate stage without going through a long process of regeneration, and have for some time little chance of gaining inclusive fitness but by helping nestmates. Once such a helper phenotype exists, natural selection can act on two newly exposed traits: first, on the efficiency of the helper phenotype at carrying out social tasks; second, on the decision mechanism governing the facultative expression of this phenotype. Both traits can now evolve so as to produce an increasingly efficient helper phenotype which will be expressed with an increasing frequency. This evolution can proceed to cross the threshold at which the helpers forego all direct fitness to form a permanently nondispersive caste, like the soldiers and workers of the present-day higher termites.

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LEARNING CAPABILITIES AND THE EVOLUTION OF CONDITION-SENSITIVE SOCIAL BEHAVIOR

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The remarkable learning capabilities of social insects have been particularly well-studied in the context of foraging behavior. Some ants, for example, perform about as well as rats in simple maze-learning tasks (1). An ability to learn olfactory cues to modify behavior is important in regulating various within-nest behaviors for eusocial insects. Learning of olfactory cues is especially important for the integrative behaviors which act as social bonds to hold societies together ("kin recognition and discrimination") (2). Learning also can be important in maintaining dominance behavior. In some *Bombus*, for example, a queen's dominance behavior is initially established by physical aggression, but later the subordinate workers avoid the queen on the basis of olfactory cues and presumably associative learning, without direct aggression (3).

Such learning capabilities may be conducive to the origins of eusociality. The Apoidea (bees and spheciforme wasps), which contains many taxa with both solitary and eusocial taxa, is an excellent taxon for examining a relationship between learning and social evolution. Social and parasitic behavior have evolved repeatedly among the bees, yet is rare in the spheciforme wasps. The ability to use learned olfactory cues for nest recognition is also widespread among solitary bees, yet is apparently rare among spheciformes (6). This ability may represent a precursor to kin recognition capabilities, possibly accounting for a biased phyletic distribution of eusociality.

A more thorough understanding of condition-sensitive social behavior requires increased emphasis on perceptual capabilities and psychological aspects of behavior, and a de-emphasis on "stereotypical" or automatic behavior.

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COOPERATIVE NEST USE IN AN AUSTRALIAN
COLLETID BEE, *AMPHYLAEUS MOROSUS* (SMITH).

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The Colletidae form the dominant element in Australia's bee fauna, comprising over 75% of described species. We report observations on a hylaeine species, *Amphylaeus morosus*, which shows surprisingly high levels of cooperative nesting during the brood-rearing period. *A. morosus* nests in a variety of substrates and habitats, eg. scapes of grasstrees in subcoastal heathland, and in dead fronds of tree ferns in temperate montane areas. The nest comprises an unbranched, lined tunnel which is provisioned with a linear series of cells. Cells often require more than one day to be completely provisioned and sealed. The bee is univoltine and a single brood is produced over spring and early summer. Adults emerge in mid to late summer, mate and then females overwinter in reused nests. A single dispersal phase occurs in early spring; new nests are founded solitarily. However, between one and three females remain in older nests which can be reused for a second or later year of brood production. About 25% of occupied reused nests are multifemale and cohabitation may persist until the end of brood production. There is no evidence that reproductive differentiation occurs among cohabiting females. Electrophoretic data indicates a mean relatedness between adult nestmates of approximately $r = 0.26$. Since adult nestmates are always from the same generation, relatedness between females and their partner's offspring should be about half this value. Consequently, it seems unlikely that kin selection is a major factor in maintaining cooperative nesting in this species. However, it is not clear that mutualistic benefits could provide an alternative explanation for cooperative nesting. The number of viable brood cells per female in multifemale nests is not significantly different from single-female nests and there is potential for nestmate parasitism. This potential is created by having to provision only one cell at a time and the opportunities for surreptitious oophagy and egg-laying.

LIFE HISTORY EVOLUTION IN SOCIAL WASPS: A POPULATION DEMOGRAPHIC PERSPECTIVE

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A potentially profitable approach to unraveling the evolution of sociality is to characterize life history traits of social and antecedent solitary forms and then focus on transitions that must have taken place. Typical life history traits of solitary wasps are that reproductive lifetimes are short and maximum fecundities low, but the probability of at least some reproductive success for a potential reproductive is relatively high. Additionally, solitary wasp taxa are almost universally protandrous. In primitively social wasps, successful reproductives have long lifetimes and high maximum fecundities, but most potentially reproductive polistines never achieve this. That is, the probability of success for a potential reproductive social wasp is relatively low, and few reproductives have positive fitness. At the same time, all but a few social wasp species are protogynous. The differences in reproductive lifespan and fecundity between reproductively successful solitary and social wasps incorporate a clear component of nourishment, other than or in addition to the nourishment of solitary taxa, that can sustain longevity and continued reproduction. Often this nourishment is garnered within the context of the social interactions of the colony. Thus the patterns of lifespan and fecundity that are typical of primitively social taxa may be more likely consequences than causes of social behavior. The shift from protandry to protogyny, however, probably coincided with, and contributed significantly to, the evolution of sociality. The ability to bias sex ratio requires a mechanism, and in Hymenoptera that mechanism is haplodiploidy. Therefore if the shift from protandry to protogyny is a threshold condition for the evolution of sociality in wasps, then haplodiploidy has been an essential contributor to that social evolution. But the contribution of haplodiploidy has been in the context proposed by Alexander (1974) and not that proposed by Hamilton (1964). The Hamiltonian haplodiploidy hypothesis is false. But the concentration of social insect taxa in a haplodiploid order is no coincidence. Haplodiploidy is not necessary for the evolution of insect sociality per se, but it is one among several features that explain the concentration of social taxa in the stinging thread-waisted Hymenoptera.

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THE EVOLUTION OF SOCIALITY IN APHIDS

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The soldier-producing aphids are the only eusocial insects that are clonal. In order to understand the evolution and ecology of the social aphids, it is helpful to take a clone's-eye view. The evolutionary events associated with the origins of sociality then become matters of resource allocation - for example, the choice between investment in defence and reproduction. In social aphids, in marked contrast to the sexual eusocial insects, there is no disagreement among colony members about investment decisions, provided that they are all clone-mates.

We present here a simple model for optimal investment by a clone in soldiers. This model predicts, for example, that a clone will be selected to increase its investment in soldiers as the colony growth rate declines and as predation increases. Some of these predictions are examined in relation to recent observations on species of *Pemphigus*.

SISTER-GROUP COMPARISONS FOR GROUPS OF SISTERS AND THE EVOLUTION OF SOLDIERS IN THYSANOPTERA

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We describe a new type of approach to combining microevolutionary and phylogenetic information for inferring the causes of the origin of social behavior. The approach involves comparing pairs of sister-taxa that differ in the behavior of interest, for all ecological, morphological, and life-history variables hypothesized to be involved in causing, allowing, or preventing the transition. If the origin of most behaviors involves multiple interacting causes, then this method may yield clearer, more direct results than comparative methods which require *a priori* designation of pairs of putatively causal and caused variables, with other factors omitted or "controlled for" statistically.

We applied our comparative approach to the phylogenetic relations (inferred from DNA sequence) and behavioral ecology of Australian gall thrips. The data suggest that three factors, (1) long-lived galls, (2) fighting between gall foundresses, (3) high levels of kleptoparasitism, are important for the evolution of soldiers in this group. Application of the approach to all eusocial forms suggest that most origins of this social system can be explained via a combination of two sufficient, but not necessary, ecological and morphological conditions.

Phylogenetic and behavioral-ecological analysis of social behavior requires that much more research effort be devoted to taxa that are *not* social, but can indicate by the pattern of their similarities and differences with their social sister-groups which variables are important in affecting behavioral transitions.

ECOLOGICAL FACTORS THAT DETERMINE THE EVOLUTION OF STERILE WORKER CASTE IN TERMITES

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No general theory explains why a sterile worker caste is not found in all species of both Hymenoptera and Isoptera (Insecta). Recent empirical findings show that, in the termites (Isoptera), feeding outside of the nest correlates well with the evolution of the sterile (true) worker caste from the non-sterile (false) worker caste. Here, we present a model that enable us to investigate the relationship between food-nest relation and true worker evolution in termites. The model analysis identifies the two ecological factors responsible for the evolution of sterile worker caste that explain the empirically shown connection between food-nest separation and true worker evolution in termites, providing a general theory on the restricted distribution of the sterile worker caste in the Isoptera. The first factor is nest stability. The model indicates that there is a critical level of nest stability above which natural selection favors true workers over false workers, irrespective of genetical relatedness. Because food-nest separation tends to increase nest stability, this theoretical result implies that the more a termite species feeds outside of the nest, the more likely its nest stability will fall above the critical level and a true worker caste will evolve. The second ecological factor is a true (sterile) worker's contribution to the reproductives' fitness. Termites, feeding on dead plant matter with a carbon to nitrogen ratio much higher than their own tissues, have to balance their C and N inputs. Two classes of C-N balancing mechanisms are possible: adding N to inputs or selectively eliminating C. Termites achieve both of these mechanisms with aid of microorganisms (symbionts). A termite can utilize food resources, thus attain productivity, only to the extent that the C-N balance capabilities of the termite-symbionts system allow. "One-piece" termites (species nesting in and consuming wood) tend not to possess C-eliminating symbionts, which are too wood-consuming for them, whereas "separate" termites (species foraging outside their nests) tend to have a full range of C-N balance symbionts. This advantage for separate termites results in their superiority in a true (sterile) worker's contribution to the reproductives' fitness, thus their evolution of sterile caste. The two factors, nest stability and true worker's contribution to the reproductives' fitness, are complementary in enhancing the evolution of sterile worker caste; thus, when combined, they explain more readily explain the connection between food-nest separation and true worker evolution in termites.

PATHOGENS AND TERMITE POPULATION BIOLOGY

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Disease risks associated with outbreeding could set limits on dispersal, and influence the extent of inbreeding in termite populations. Rosengaus and Traniello (1993) suggested that termites may exhibit genetic or humoral immune responses to pathogens; through individual immune responses and/or social interactions, colony-specific immunities could occur. By innoculating termites with small dosages of toxins or entomopathogenic fungi, and subsequently challenging them with lethal dosages, we have begun to determine if termites have immunological memory. This information will help clarify the nature of termite adaptation to disease. We are also estimating pathogen-related stress from the degree of fluctuating asymmetries (FA). FA may often show positive correlations with a number of important pathogens and may be negatively correlated with pathogen resistance (Watson and Thornhill, 1994). Also, FA seems to be negatively correlated with protein heterozygosity, both within and between populations. FA therefore, could be a potential indicator of the degree of genetic variation and the extent of inbreeding in termite populations. Through these two methods, we may be able to establish the relationships among termite immunology, population biology and sociobiology.

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POLYGYNOUS AND MONOGYNOUS FOUNDATION IN *POLISTES* : THE INFLUENCE OF PREDATION IN A STRUCTURAL ASSORTMENT MODEL ("Pal selection").

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In the frame of Hamilton's model, M.J. West has demonstrated that a female can benefit from joining a colony as an auxiliary rather than founding by herself. Although the stability and maintenance of extant social systems is appropriately explained by kin directed altruism, it is a rather complicated trait : it involves kin recognition, the altruistic trait, the decision to help only kin, and for the recipient the traits involved in the acceptance of help. To explain the original appearance of altruism, we proposed in a previous paper (1) a model of structural assortment in *Polistes* based on a single new trait with consequences on the behavior of both dominant and subordinate. The model shows that polygyny may appear and be stable even against cheaters. After such an initial establishment, kin related traits may be selected and lead to the present systems. Here we will investigate the equilibrium between potentially polygynous and strictly monogynous phenotypes. In particular, we show in a metapopulation model that the final outcome is conditioned by the rate and form of predation. According to the strategy of the predator, the population can evolve towards strict monogyny or complete potential polygyny. The predictions of the model are compared with the biogeography of polygynous versus monogynous *Polistes* species

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SYMBIOSIS: PARASITIC AND BENEFICIAL ASSOCIATIONS AMONG SOCIAL INSECTS - INTRODUCTION

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Long ago, William Wheeler believed nature was "burdened with parasitism," yet he also viewed social insect colonies as cooperative "superorganisms." These opposing views of natural organizations have always been influential in shaping the kinds of questions biologists ask, and form the conceptual core of this symposium. We restrict the term "symbiosis" to describe mutually beneficial associations, and use the term "parasitism" to describe an association in which one individual gains at the expense of another. By juxtaposing symbiosis and parasitism, we hope to better understand the conditions under which biotic associations evolve towards obligate conflict or cooperation.

Insect colonies are valuable resources because of the large labor force and large quantities of stored food. Such resources invariably attract many predators and parasites. Due to limitations in space, we regret that we have restricted this symposium to social or labor ("slave-making") parasites, and have not included many interesting and important studies on parasitic flies, beetles, and the like. Social parasites are often closely related to the host taxa upon which they are dependent, and conflict arises because parasitism is detrimental to host fitness. Parasitism has evolved repeatedly among social insects (bees, ants, paper wasps, and thrips), with the curious exception of the termites. Important new findings address mechanisms of host recognition by parasites, how parasites gain entry and integrate themselves into the host colony, and the effects of parasitism on the reproductive output of the hosts.

In our troubled political times it is too easy to view our world as rife with conflict, to view nature as "red in tooth and claw," and ignore the mutually beneficial relationships which are widespread among diverse creatures. A consideration of symbiosis--cooperation arising out of competition--shows how dependency on another species can have reciprocal benefits. We have touched on only a few examples of symbiotic relationships involving social insects, but these recent examples from different taxa nicely illustrate the benefits derived from investigating symbiosis at diverse levels of organization- from physiology to ecology to phylogeny. Taken together, these findings shine much light on the evolution of cooperation and conflict.

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REARING OF PARASITIC ANTS WITH NON-NATURAL HOST SPECIES

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Parasitic ants evoke interest because of particular life habits and often unusual features such as queen polymorphism, workerlessness and inbreeding, which all can best be studied with rearing them in the laboratory. Supplying parasite colonies with sufficient hosts is sometimes problematic. Successful experiments have been made to replace the natural hosts with easily available other species. We were able to rear *Formicoxenus nitidulus* with *Leptothorax acervorum* (Buschinger 1976). The proportions of gynomorphs and intermorphs in their offspring remained unaffected, queen polymorphism thus is not influenced by the natural *Formica* hosts. Eight *Epimyrma* species including active slavemakers (*E.algeriana*), degenerate slavemakers (*E.kraussei*) and workerless species (*E.adlerzi*, *E.corsica*) all are bred with *Leptothorax unifasciatus*, one of the natural hosts of *E.ravouxi*. The foreign host species does not affect caste differentiation, workerlessness is apparently genetically determined (Buschinger 1993). In the slavemaker *Chalepoxenus muellerianus*, replacement of the host, *L.unifasciatus*, by *L.recedens* changes the host selection behavior of *Chalepoxenus* queens and workers (Schumann, this Congress). Non-natural host species have different suitabilities for a given parasite, hence the experiments also can reveal mechanisms related to host specificity. The results demonstrate that rearing parasitic ants with non-natural hosts not only facilitates their laboratory culture but is also a powerful tool for investigating their life habits, particular polymorphisms and other features. It appears worthwhile to extend these studies on more parasitic and potential host species.

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DETECTION AND CHOICE OF THE HOST NEST IN OBLIGATE SOCIAL PARASITES OF *POLISTES*

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The loss of nest founding capacity in obligate social parasites has led them to develop the ability to locate a host nest to usurp. A parasite female can usurp the first nest she comes across, or choose the best among those available. In addition, as in other insect social parasites, host specificity in *Polistes* differs in degrees: *P.sulcifer* exploits only one host while *P.semenowi* and *P. atrimandibularis* seem to be more generalist. This study attempts to determine which factors influence the detection and choice of usurpable nests, as well as host-specificity in *Polistes* parasites. In the first experiments, *P.sulcifer* females were tested in a glass box containing a whole nest or in parts (paper material or immature brood), hidden by an opaque, porous screen. Results show that *P.sulcifer* females can locate and recognize a host nest by its odour without actual contact. The experimental boxes were too small to allow the distance from which the parasites could perceive the nest odour to be determined. In other experiments *P.sulcifer* females were exposed to binary choice between nests of different species, nests of the same species but of different dimensions or stage of development, and with or without an adult host. These experiments confirm the monospecificity of *P.sulcifer* for *P.dominulus* and reveal that the females of this parasite prefer larger nests in a later stage of development, corroborating field observations. Data indicate that the presence of an immature brood is determinant in choosing which nest to usurp. Its adaptative significance is clear. Choosing the right nest to usurp, thus avoiding unnecessary risks and saving time, will maximize the reproductive success of the parasite. The present data indicate that *P.sulcifer* can easily locate and choose which nest to usurp. Host preference experiments with *P.atrimandibularis* show that this species does not discriminate between nests of its two hosts and that it prefers the nests of *P.nimpha*. Similar studies on all three species of social parasites, which moreover exhibit different behavioural traits, could help understand the relationship between them.

LEVELS OF SOCIAL PARASITISM OF THE
ALLODAPINE BEE *EXONEURA BICOLOR* (SMITH) BY
THE CUCKOO BEE *INQUILINA SCHWARZI* MICHENER

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The bee tribe Allodapini is notable for its repeated independent origins of social parasitism (Reyes and Michener 1990). One example is that of the Australian native allodapine bee *Exoneura bicolor*, which is semisocial, and is parasitised by the allodapine brood parasite *Inquilina schwarzi*. This study examines aspects of the *Inquilina-Exoneura* relationship. Over the period of seasonal activity, dead tree fern fronds containing intact colonies of *Exoneura bicolor* were collected from a wet montane habitat in South-Central Victoria and nest contents recorded. Immatures from one collection late in the brood rearing season were subjected to allozyme electrophoresis in order to distinguish brood of the host from that of the parasite. In parasitised nests, the proportion of parasite brood was found to be highly variable. The study also showed that *Inquilina* shows no preference for larger or smaller colonies. A significant difference was found detected between the number of eggs per female in parasitised nests and the number of eggs per female in unparasitised nests. This is most likely due to the parasite consuming, on average, fewer eggs than she lays. It was also found that significantly more newly-founded nests were parasitised than nests which had been founded in a previous season and were re-used. Reasons for this could be a higher susceptibility of new nests, a host strategy of abandoning previously-parasitised nests, or a parasite oviposition strategy of parasitising newly founded nests, to better utilise the period of maximum oviposition rate of the host population.

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COLONY FOUNDING IN THE EUROPEAN AMAZON ANT
Polyergus rufescens Latr.

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Queens of obligatory socially parasitic ants are not capable of founding new colonies independently. Therefore, newly-mated females of the dulotic genus *Polyergus* invade host-species nests (belonging to the genus *Formica*) and usurp the role of reproductives. To locate a host colony, *Polyergus* females may take part in slave raids. This is an advantageous strategy also to penetrate target nest, since the invasion is facilitated by the panic and disorganization induced by raiding swarms (Topoff, 1990). In this research, the process of host colony take-over by queens of the European amazon ant *Polyergus rufescens* was analysed in the laboratory. Newly-inseminated females were individually introduced into queenright and queenless artificial colonies of both *F. cunicularia* (the slave present in the natal dulotic nest) and *F. rufibarbis* (another potential slave). The parasitic female was almost always adopted in the colonies of *F. cunicularia*, whereas in the presence of *F. rufibarbis*, the alien queen was generally killed in a short time. These data show that the slave-making queen, before laying her eggs, must kill the resident queen, become accepted by the resident workers and appropriate the host brood. Moreover, the results confirm the high level of aggression displayed by *F. rufibarbis* towards *P. rufescens* and are discussed in relation to the host specificity typical of this slave-maker (Mori *et al.* 1994). Since our previous field observations showed that usually more than one mated female participate in slave-raids and penetrate together the same target colony, pleometrosis could occur. Therefore, laboratory experiments were conducted by introducing simultaneously two newly-inseminated *P. rufescens* females into colonies of *F. cunicularia*. When adoption was achieved, only one dulotic female survived, the other being killed by the resident workers. These data are consistent with the strict monogyny characteristic of the majority of the obligatory slave-making ant species. Finally, the egg-laying by a *Polyergus* successful usurper and the subsequent eclosion of her brood (that was perfectly integrated in the artificial mixed colony) was observed.

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THE DIGESTIVE SYMBIOSIS IN ISOPTERA

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Beside cellulose which constitutes the main polysaccharide in plants, there are other polysaccharidic components such as hemicelluloses (xylan, galactomannan, arabinogalactan...). fungic components (nigeran, pullulan, glycogen) lignin, pectins or starch. All these substrates are hydrolysed by some specific enzymes to give monosaccharides which are used for the metabolism of living organisms. Therefore plant material has some nutritive value only for those insects which produce a set of glycosidases. This property is share by termites wich possess a set of enzymes in their digestive tract, allowing optimum utilization of the plant material ingested.

The digestive ability of termites to degrade plant material is due to symbiotic relationships with various microorganisms in their gut. Therefore, termites hindgut possess many symbionts the diversity of which is strictly correlated with isoptera evolution.

The symbiotic microflora of wood eating "lower" termites include flagellates, and some bacteria. In higher termites (Termitidae), the flagellates are not present anymore and the hindgut contains only a dense and diverse bacterial community. Among Termitidae, the fungus growing termites present a genuine double symbiosis ; endosymbiosis with gut microflora and exosymbiosis with a fungus from the genus *Termitomyces*.

Despite the fact that this symbiotic relationship is essential to termite nutrition, the endogenous capacity of termite to degrade plant material is certainly more important than it was previously thought. Thus this work will give new data on the real importance of symbionts (protozoa, bacteria and fungus) for termites digestive metabolism.

FACULTATIVE AND OBLIGATE SLAVERY IN FORMICINE ANTS:
RAIDING EFFICIENCY AND BEHAVIORAL REPERTOIRER. Savolainen¹ and R. J. Deslippe²¹Museum of Comparative Zoology, Harvard University, 02138 Cambridge MA, USA²Department of Zoology, University of Alberta, Edmonton, Canada T6G 2E9

Slavery is a form of social parasitism in ants. Slave-making ants raid nests of closely related ant species, capture the developing offspring and rear them to slave workers. In the Formicinae, species of the *Formica sanguinea* group are facultative slavemakers and those of the genera *Polyergus* and *Rossomyrmex*, obligate slavemakers. We tested three hypotheses: (1) The more frequent slavery is in a species, the higher the proportion of slaves, and thus (2) the slaves should feature as an extra caste within the nest of the slavemaker. (3) Those formicine slavemakers that virtually always have slaves, are obligate slavemakers. In Elk Island National Park in western Canada, the facultative slavemakers *Formica subnuda* and *F. subintegra* and the obligate slavemaker *Polyergus breviceps* enslaved the same species, *F. podzolica*. For every ten *F. podzolica* mounds we found one *F. subnuda* nest, whereas three and one percent of all *F. podzolica* mounds examined were parasitized by *F. subintegra* and *P. breviceps*, respectively. One third of the *F. subnuda* nests had slaves, whereas all nests of *F. subintegra* and *P. breviceps* contained slaves. The proportion of slaves, when present, varied between 1-30% in the nests of *F. subnuda*, and between 70-90% in the nests of the other species. The slaves of *F. subnuda* were significantly smaller than those of the other slavemakers indicating that they were raided from relatively small nests. *F. subnuda* managed all its colony tasks alone. Raiding was the main activity outside the nest of *F. subintegra* and *P. breviceps*. They never foraged, but later in the summer *F. subintegra* attempted to plug nest entrances at night but without success. In laboratory experiments, when deprived of slaves, *F. subintegra* carried pupae into the nest, but it was slow and inefficient in completing the task. *P. breviceps* workers never touched the pupae. We conclude that *F. subintegra* is an obligate slavemaker and closely resembles *P. breviceps* in slavemaking. Contrary to *P. breviceps*, *F. subintegra* has retained some of its domestic behavioral repertoire. However, the repertoire is insufficient for *F. subintegra* to carry out the colony tasks. Thus, slaves of *F. subintegra* and *P. breviceps* function as a worker caste in the colony: the slaves forage, maintain the nest and presumably nurse the brood. These findings corroborate our hypotheses.

IMPRINTING EFFECTS ON HOST SELECTION BEHAVIOR OF THE DULOTIC ANT *CHALEPOXENUS MUELLERIANUS* (FINZI)

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Early experience is known to influence the brood care behavior, and to induce nesting preferences of several ant species. However, scanty information is available concerning imprinting effects on the host choice of dulotic ants. In arena experiments, the Mediterranean slavemaker *Chalepoxenus muellerianus* was investigated. Test colonies were taken from a population exclusively parasitizing *Leptothorax unifasciatus* ("L-colonies"). In the laboratory, queens and workers of different imprinting types were produced by removing the *L.uni.* workers and replacing them by a potential host, *Temnothorax recedens* ("T-colonies"). The slavemakers then were given a choice between *L.uni.*, *T.rec.*, a non-host species (*L. nylanderii*) and an empty control nest. Host selection was studied during colony foundation of newly inseminated females, and in the raiding behavior of workers. The results showed clear evidence for imprinting-like processes. The host species present in the nest strongly influences the host choice of *C. muellerianus* females and workers. Larvae are receptive to species-specific stimuli as well as callows. However, *L.uni.* kept very attractive even when excluded during the ontogenetical development of the parasites, indicating a genetical component of host specificity. Imprinting presumably strengthens the existing genetical linkage to a certain host species. On the other hand, imprinting may facilitate a change of host species (e.g. after a casual colony foundation in a potential host species nest), enabling the colonization of habitats, where the main host is absent or rare.

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THE MIGRATING HERDSMEN ANTS OF SOUTHEAST ASIA: A SPECIES-RICH COMPLEX OF TROPHOBIOTIC SYMBIOSES OF DOLICHODERUS ANTS AND THEIR MEALYBUGS (HOMOPTERA: PSEUDOCOCCIDAE: ALLOMYRMOCOCCINI)

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In their study on *Dolichoderus cuspidatus* in Malaysia, Maschwitz & Hänel (1985) described a completely new mode of life in ants which they called "migrating herdsmen" or "true nomads": the ants are living in an obligatory and species-specific trophobiosis with certain highly polyphagous mealybugs which they transport to new host plants and also keep in their bivouac-like nests. Colony movement behaviour, colony reproduction and queen morphology are strongly modified as an adaptation to this symbiosis. In our studies we found that the migrating herdsmen lifestyle is common and widely distributed in SE-Asian *Dolichoderus* ants. It is a symbiosis of partners belonging to two species-rich and presumably monophyletic groups: a species-group of *Dolichoderus* and the anomalous pseudococcine tribe Allomyrmococcini. We demonstrated a nomadic lifestyle for at least 11 partly new *Dolichoderus*-species in association with 23 species of 9 partly undescribed genera of Allomyrmococcini. In some mountain regions they are the dominant arboreal ants. In some places like NE-Borneo we found five syntopic migrating herdsmen systems. Possible modes of niche differentiation will be discussed. The different species show many modifications of the *D. cuspidatus* lifestyle, e. g. in the mode of mealybug transport behaviour, nesting behaviour, colony size, trail system and activity patterns. In some montane populations of nomadic *Dolichoderus* we found evidence of a secondary loss of their typical allomyrmococcine herdsmen mealybugs.

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MEALYBUG-TRANSPORT BY SWARMING QUEENS, WATER
BAILING FROM FLOODED NEST CHAMBERS, AND OTHER
ADAPTIVE STRATEGIES OF A SOUTHEAST ASIAN BAMBOO
ANT (HYMENOPTERA: FORMICIDAE:
PSEUDOMYRMECINAE: *TETRAPONERA*)

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Bamboo with its hollow internodes is utilized as habitat by many generalist arboreal ants. Interestingly, a few species of ants have become obligate bamboo specialists, among them an as yet undescribed *Tetraponera* sp. near *attenuata* F. Smith (*T.* sp. PSW-80 in the collection of P. S. Ward, University of California at Davis). This ant inhabits the stem internodes of at least 3 spp. of large bamboo, including *Gigantochloa scortechinii* Gamble (up to 25 m tall, 10 cm diameter), the most common host plant at our main investigation site, the Ulu Gombak Field Studies Center near Kuala Lumpur. The large monogynous colonies may occupy dozens of internodes in different culms. Only internodes with small access holes are inhabited that can be blocked by one to a few workers to ward off potential intruders. During heavy rainstorms, runoff-water may flow into the internodes through the entrance holes. *T.* sp. responds with an effective countermeasure: The workers ingest the liquid and regurgitate it to the outside until no standing water remains. *T.* sp. apparently derives much of its food requirements from the honeydew of its symbiotic pseudococcids, *Kermicus wroughtoni* Newstead, which are kept inside the internodes. The close symbiosis of *T.* sp. with *Kermicus* becomes particularly apparent during the mating flight: The young queens carry *Kermicus* crawlers along in their mandibles for colony foundation. Unlike many other Pseudomyrmecinae, *T.* sp. does not exhibit predatory behavior but instead scavenges decaying plant matter, feces and dead arthropods. There are also extended periods with no outside foraging. In contrast to other pseudomyrmecine plant specialists that reach comparable colony sizes, *T.* sp. is unaggressive and does not defend its host. Several species of spiders and the specialized staphylinid beetle *Orphnebius politus* are important predators of *T.* sp.

ROBBER BEES AS ARMY ANTS

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Lestrimelitta limao is the most common of the seven known robber bees. These bees never visit flowers and take brood provisions, nest material and honey from inside nests of other stingless bees, and opportunistically rob honey from Apis mellifera. Studies by Sakagami et al. (1993) established that daily robbing and foraging involve both mass raids and low-level raids of only a few bees. Simultaneous raids can take place on several host colonies, and the duration of a raid varies from a few hours to days. Queens and workers of host colonies are largely undamaged, but brood provisions are removed completely. Field observations and computations based upon available host colonies preferred by L. limao in natural forest indicate that it is a prudent parasite, and very similar in tactics to the Neotropical army ants, Eciton, in harvesting social insect hosts without overexploitation. Contrary to the army ants, however, colonies of Lestrimelitta are stationary in location, and occasionally reproduce by usurping a host nest. When a foreign colony of L. limao is introduced near an established conspecific nest, mortal combat quickly results, escalating to colony death without nest usurpation if colonies are unevenly matched. This experiment, and apparently ritualized contests between rival colonies, strongly suggest that populations of L. limao are self-regulating. Further evidence for the periodic harvest strategy of L. limao is derived from life history data on its preferred hosts colonies, Scaptotrigona and Nannotrigona, and their natural nest densities in forest. If L. limao at normal nest density uses all host colonies within foraging range, it can perform a mass raid on each colony once every 15 days — approximately the egg-to-pupa period for stingless bees. This amount of time is the minimum needed recovery period for colonies that have their entire young brood population removed when cell provisions are taken.

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COMMUNICATION IN HONEYBEES

INTRODUCTION

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The first section of the symposium is devoted to analyses of the effects of chemical signals on social organisation in *Apis mellifera*. The presentations deal with the interaction between queens and workers, the control of swarms, the interaction between workers and brood, and the variability of chemical secretions between races. The primer and releaser effects of the queen mandibular gland secretions are explored by Winston. Using a model nesting cavity, Shen and Schmidt have been able to demonstrate the effectiveness of Nasonov pheromones in swarm attraction and its interaction with queen pheromone in the process. Regulation of processes of brood care and worker reproduction are the subject of Trouiller's contribution. Variations in the queen pheromone composition in different populations of honey bees are explored by Crewe in order to determine whether social parasitism by Cape honeybee workers can be explained on the basis of these differences.

The second section of the symposium is focused on recruitment communication in honeybees. Kirchner will address the question how much the dance information and chemical cues contribute to the site specific recruitment of honeybee foragers. Visscher studied a similar question on the colony level: what is the benefit of dance communication for the colony? Dreier will report on comparative studies of the sensory basis of dance communication in Western and Asian honeybees. Sound signals of *Apis cerana* will be described by Sasaki. The significance of the tremble dance of honeybee foragers for the regulation of nectar collection and nectar storage will be discussed by Seeley.

THE ESSENCE OF ROYALTY: HONEY BEE (*Apis mellifera*) QUEEN PHEROMONE

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Honey bees, like most highly eusocial insects, use pheromones to communicate. However, the honey bee is the only social insect for which a primer pheromone has been identified. This pheromone consists of a five-component blend of acids and aromatics produced in the queen's mandibular glands, and is involved in both primer and releaser functions. The pheromone blend is picked up by worker bees attending the queen, and moved through the nest as a unit via worker-worker interactions and deposition by workers and the queen on comb. The pheromone is highly attractive to worker bees, and also may influence foraging choices for nectar vs. pollen, both of which can be considered releaser functions. However, the same pheromone blend inhibits queen cell production in colonies, and can influence hormonally-based temporal caste ontogeny, both primer functions. In addition, synthetic queen mandibular pheromone has proven very effective in commercial applications for beekeeping and crop pollination.

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CHEMICAL COMMUNICATION IN REPRODUCTIVE DISPERSAL OF HONEY BEES (APIS MELLIFERA)

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Swarm-founding reproduction in social species presents a difficult communication problem not faced by species having solitary, independent, or multiple-foundress modes of reproduction. To achieve successful reproduction, swarm-founding species must have communication systems to coordinate the activities and movement of often thousands of individuals from one nest site to another. Honey bees have the added requirement that their future nest must be especially safe and protected from a multitude of potential predators who are ever ready to plunder these brood and honey reserves -- the richest of all insect food caches. Thus, honey bees must discover a protective and sturdy nest cavity, then must communicate this information to all the members of the dispersing swarm. Pheromones are key to this communication. To characterize the importance of pheromonal communication in the reproductive dispersal of honey bee swarms, we first had to eliminate the confounding variable of nest cavity suitability. This was achieved by developing an idealized hollow tree made of molded wood fiber that was highly acceptable to honey bee swarms. By using these artificial nest cavities in direct choice tests, we were able to demonstrate: 1) that synthetic Nasonov pheromone-containing artificial nests were preferred to those without the pheromone; 2) that attractiveness of the pheromone increases with effluvia concentration over at least the 25-fold range tested; 3) that a 5-component pheromone blend containing nerolic and geranic acids was more attractive than the 3-component blend without those acids; 4) that a 5-component blend of synthetic queen pheromone played no role in attraction of reproductive swarms to nest sites; and 5) that Africanized honey bee swarms are attracted to the same Nasonov pheromone blend as European bees, but they exhibit different parameters for nest cavity acceptance. In crossover design experiments, Nasonov pheromone was clearly demonstrated to attract swarms to artificial nests; in contrast, queen pheromone serves no role in the reproductive dispersal process except as an indication of queen presence and as a synergist for swarm clustering. The discoveries from this investigation are currently being used by private businesses for trapping and eliminating unwanted Africanized bee swarms, and for capturing European swarms.

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THE RELEASER AND PRIMER EFFECTS OF BROOD ON WORKERS IN HONEYBEES

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In honeybees (*Apis mellifera*), brood is involved in both releaser (brood care) and primer effects on adult workers. Despite many studies have been performed with live brood, the role of semiochemicals in the complex interactions between brood and workers is poorly understood. Pheromonal compounds involved in incubation, capping and nutrition behaviors have been identified. Methyl and ethyl fatty acids esters secreted by larvae of different ages and castes seems to control, at least partly, these two last behaviors. Brood has also an important role in the control of worker physiology. The inhibition of worker ovaries is controlled by brood and by queen secretions, and the hypopharyngeal glands development of workers of any age is increased in presence of larvae. The relative importance of esters and others pheromonal compounds in the control of these two physiologic parameters will be discussed.

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DIFFERENTIATION OF CHEMICAL SIGNALS IN POPULATIONS OF AFRICAN HONEY BEES.

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The mandibular gland products of honey bee queens can be mimicked by a synthetic five component blend¹. Although this blend does not regulate ovarian development², its effectiveness in eliciting retinue behaviour may in part be responsible for allowing workers of the Cape honey bee (*Apis mellifera capensis*) to parasitize colonies of other populations of honey bees³. This parasitism being effected by the queen-like blend of components produced by these workers. The geographic variation in the relative proportions of the major components of the mandibular gland secretions of queens and workers from colonies of *A. m. scutellata*, *A. m. capensis* and their natural hybrids from 11 localities in South Africa were analysed gas chromatographically. This analysis confirms that 9ODA predominates in secretions from Cape queens⁴ and that it occurs universally in Cape workers⁵ even though these workers are not false queens⁶. Hybrid colonies produce two classes of workers, those that are *scutellata*-like and in which 10HDA predominates and those that are *capensis*-like and in which 9ODA predominates even in queenright colonies. Additional aromatic components are present in *capensis* secretions.

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MECHANISMS OF RECRUITMENT COMMUNICATION IN HONEYBEES

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Honeybee foragers recruit nestmates to profitable food sources. On return to their nest, successful foragers perform dances, which contain information about distance and direction of the food source. Classical studies by von Frisch indicated that both, the dance information about distance and direction, and odour cues are used by the nestmates to find the food source. However, experiments performed by Wenner in the 1960s seemed to indicate that bees exclusively rely on odour cues and do not make use of the dance information at all. The significance of the dance language was later demonstrated by Gould in the '70s. Recent experiments (reviewed in Kirchner 1993) involving a robotic bee, which recruited site-specifically, and other new experimental approaches confirmed that bees indeed use the dance information to find food sources and showed that they use airborne sound signals emitted by the dancers and a sense of hearing to perceive the dance information in the darkness of their nest. Wenner, however, insists in recent publications (see Wenner et al. 1991) on the view of recruitment in honeybees being exclusively based on an odour search strategy. I will therefore review old and new evidence for the use of the dance information by recruit bees as well as evidence for the use of odour cues and report about a series of experiments, which allow to assess the relative significance of dance information and odours for the site specific search of recruit bees. In these experiments recruit bees were trapped automatically in arrays of artificial flowers at various distances from the hive. The distribution of directions in which the recruits searched for food was compared between food sources which were artificially scented or unscented, and also compared between recruitment by dancers performing well oriented dances on the vertical side of the comb and dancers performing disoriented dances on a horizontal comb. The results show quantitatively that bees use both, odour cues and the dance information. Odours are of some influence, even when the food source is far away from the hive. However, the larger the distance, the higher the relative significance of the dance information. At 750 m of distance the mean angular deviation of the directions in which the recruits searched for food from the direction of the advertized food source was 71° , when bees exclusively relied on odour cues, but only 11° , when they could make use of the dance information about the direction of the food source. The results falsify Wenner's exclusive odour search hypothesis.

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FITNESS THROUGH DANCING? EFFECTS OF RECRUITMENT COMMUNICATION ON FOOD COLLECTION BY HONEY BEE COLONIES

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This study aims to directly assess the contribution which possession of a dance language recruitment system makes to the food collection of honey bee (*Apis mellifera*) colonies. Matched colonies were established with three treatments: vertical observation hives, and horizontal observation hives with either diffusely-lit translucent domes or directionally-lit transparent domes. The mass of each colony was monitored every 30 min by an electronic balances on which the hive was mounted. Results were analyzed by ANOVA to factor treatment, date, and colony effects. Colonies in horizontal hives lacked the usual gravity reference for the directional component of the waggle dance. Horizontal colonies gained significantly less weight than similar vertical colonies. Dances in diffusely-lit horizontal hives were disoriented, while dances in hives with directional lighting were more oriented, but still inconsistently so, and much less precisely oriented than in vertical hives. There was not a significant difference between diffusely and directionally lit hives in terms of the increase of mass. Mapping of locations communicated in dances showed that floral resources in the study area are abundant but quite dispersed. In this environment, matched adjacent colonies differed substantially in foraging distribution and distance. The results of these studies are equivocal regarding effects of the dance language on food collection. The differences in gain of mass between horizontal and vertical hives may have been due to disorientation of foraging associated with the absence of gravity cues for dancing bees, or to other factors associated with the unnatural horizontal combs. The two horizontal hive treatments, which were designed to factor these differences, did not show a difference, but the treatments were imperfect, principally in regard to the orientation of dances in the directionally-lit hive. The ecological setting of this study might also make dance language communication less important. Environments with scarce and more patchy resources would be expected to result in stronger differences. This study is continuing, with comparisons in different environments and seasons, and improved directional lighting.

HOW HONEYBEES PERCEIVE THE INFORMATION OF THE DANCE LANGUAGE

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The ability of honeybees to share information about feeding sites greatly helps their colonies to achieve high efficiency in foraging. The principal mechanism of this recruitment communication is the waggle dance, which is performed in all species of the genus *Apis*. Whereas dancing behavior has been studied extensively, little was until recently known about the behavior of those bees which are recruited to the food source and about the sensory channels used by different species for information perception. In *Apis mellifera*, previous studies of the recruitment rate to artificial feeders revealed that only the minority of the bees which have been observed attending dances actually find the feeder. I will report comparative observations and experiments focusing on the behavior of follower bees and how it correlates with their success. Continuously videotaping of individually tagged follower bees from first contact with the dancer until the arrival at the feeder showed that the behavior of dance attenders varies greatly. By comparing behavior of successful follower bees with unsuccessful bees it turned out that information transfer apparently takes place only during continuously following the dancer for several waggle and return runs. Tactile interactions between dance attenders and dancers were analyzed using high-speed-video-recordings. In *Apis mellifera*, which dances in the darkness of the hives, tactile interactions between dancer and follower occur more frequently than in *Apis florea*, a honeybee species dancing in the open on top of the comb under day light. Thus, a tactile mechanism for information transfer seems to be possible in the European bee, but not in the dwarf bee *Apis florea*. On the other hand, it has been shown in *Apis mellifera* that near field sound signals produced by the dancer during waggle run provide the information about the location of the food source. The follower bees are able to detect those sound signals, which are perceived using Johnston's organ, a chordotonal organ located in the pedicel of the antennae. To determine whether tactile signals and/or sound signals are used by the follower bee for picking up the dance information, ablation experiments with individually marked follower bees were conducted. It could be shown that in *Apis mellifera* disturbing of tactile interaction by removing the antennal tips of the follower bees had little or no effect on communication success, whereas disturbing the acoustical perception by removing one antenna reduced the communication success. In *Apis dorsata*, the giant honeybees, which like *Apis florea* can use visual cues for information transfer, but also produces sound signals, the latter manipulation of the follower bee had no effect, indicating that this species is at least at daytime not as dependent on sound signals for dance communication as *Apis mellifera*.

ADAPTIVE ALTERATIONS OF THE COMMUNICATIVE SOUND/VIBRATIONS IN ORIENTAL HONEYBEE, *APIS CERANA*

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Sound/vibrations are widely used as communicative measures in the oriental honeybee, *Apis cerana*. We recorded the sound/vibrations emanated during grooming dance, dorso-ventral abdominal vibration (DVAV), foraging dance, absconding dance, checking intruder bees, abdomen shaking, shimmering, queen piping, worker piping, and trembling dance. On the basis of comparison of those monitored by video system and their wave-form analysis, some interesting adaptive alterations exploited in *A. cerana* were examined.

1) **Geographic cline of distance code in foraging dance sound:** Both *A. cerana* and *A. mellifera* allocated same length of dance-sound signals to longer distance in north-adapted subspecies or biotypes. For instance, *A. cerana japonica* and *A. mellifera carnica* exploited similar grade of code.

2) **Quantitativeness and continuity of the dance information to inform food sources near hive.**

3) **Absconding dance as a modification of foraging dance:** Extraordinary long tail-wagging sound seemed to have a new meaning, "relocation of the present nesting site".

4) **Hypothesis on the differentiation of abdomen shaking and shimmering:** Prototype body shaking might evolve, in one way, to cooperative visual display against predator hornets like in *A. laboriosa*. Similar response was seen, probably as remnant behavior, in *A. cerana* which became cavity nester. Abdomen shaking against predator seen around the nest entrance appears to be derived also from prototype body shaking in curtain bees. Individual distribution on solid substrates, not on the bee curtain, inhibits the chain reaction, and consequently, associated sound has no more practical meaning. Shimmering (hissing) evolved, as another way, to amplify the alarm-sound effect against predators by making it in concert. Body movement in shimmering bees as visual display is minimized in dark cavity condition.

THE TREMBLE DANCE OF THE HONEY BEE: A SIGNAL
FOR THE COORDINATION OF TWO CASTES

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An important feature of the organization of nectar collection by honey bee colonies is the division of labor between the *foragers*, who work outside the hive gathering the nectar, and the *food storers*, younger bees who work inside the hive processing the nectar. This division of labor boosts the efficiency of a colony's energy intake, but it also creates a problem of coordination within the colony since the rates of nectar collecting and processing must be kept in balance for the two-stage operation to proceed smoothly. One of the mechanisms of feedback control whereby a colony keeps nectar collecting and processing in balance is the tremble dance. It has been shown experimentally that a forager will reliably perform this dance if she visits a highly profitable nectar source but upon return to the hive experiences great difficulty finding a food storer to take her nectar. It has also been shown experimentally that the performance of tremble dances is followed quickly by a rise in a colony's nectar processing capacity (Seeley 1992) and by a drop in a colony's recruitment of additional bees to nectar sources (Kirchner 1993). Hence it appears that the tremble dance functions as a mechanism for keeping a colony's nectar processing rate matched with its nectar intake rate at times of greatly increased nectar influx. Evidently the tremble dance restores this match in part by stimulating a rise in the processing rate, and in part by inhibiting any further rise in the collecting rate. Experiments are planned for the summer of 1994 to investigate exactly how the tremble dance effects a rise in the processing rate. Does this involve increasing the number of food storers, or increasing the work rate of food storers, or both? If tremble dances boost the number of food storers, then who are the additional food storers? The results of these studies will be reported in Paris.

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HOW THE SUGAR FLOW OF THE EXPLOITED SOURCES AFFECTS THE TROPHALLACTIC BEHAVIOUR DURING RECRUITMENT IN HONEY BEES

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A honeybee forager can stimulate other members of its colony to resume foraging at a known food source without dancing [1]. A possible communication channel could be the trophallactic behaviour (mouth-to-mouth food exchange contacts). Through trophallaxis bees can communicate characteristic properties of the source like odour [2]. Furthermore, it is known that crop loads of foragers depend on sugar flow rates at the food source [3] so that bees could represent this factor while unloading in the hive. Honeybee foragers were conditioned to collect food at an automatic feeder with regulated flow rate of 50% w/w sucrose solution (range: 0.76-7.65 $\mu\text{l}/\text{min}$). Bees returned to an observational hive where their behaviour was recorded. Increasing the sugar flow rate caused the frequency of unloading contacts ($F=5.554$; $df=3,210$; $P<0.001$; ANOVA-test) and the rate of the transferred sugar to increase ($F=3.397$; $df=3,194$; $P<0.02$). After unloading, foragers often approach other nest mates and beg for food before returning to the food source. Begging behaviour was also modified with the flow rate at the food source, being less frequently for higher sugar flows ($F=3.732$; $df=3,181$; $P<0.02$; ANOVA-test). These results show that returning foragers modulate their trophallactic behaviour depending on the profitability of the food source they presently exploit. Through the food exchange behaviour, the forager could increase not only the recruiting effect by the number of stimulated potential foragers when its source is profitable, but it could carry out more "direct contacts" with other exploited food sources (through begging) when the exploited source is sparse.

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EXOCRINE GLANDS AND SOCIAL ORGANIZATION

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Social insect colonies are well known for their high degree of organization, in which every individual member contributes to the success of the community. Exocrine glands play a very important role in the proper functioning of these societies, as is reflected at all levels in the social organization. As a result, social insects can be considered as tiny walking or flying glandular batteries, in which so far 63 different glands are known, that elaborate an overwhelming variety of exocrine secretions. Although in several cases the precise function of a particular gland remains unknown, the well known role of many others illustrates their obvious importance. They function, among others, in the elaboration of antibiotics and nesting materials, of digestive enzymes, of caste determining substances, and in chemical defense. The secretions of some glands are currently considered to be cues in colonial or species recognition. The by far best analysed and most diverse role of exocrine secretions is their adaptive function in inter-individual communication. Individual glands mostly release multicomponent signals, which in complex behavioural activities such as food recruitment may play distinct roles according to the needs of a colony.

The study of exocrine glands mainly involves morphological, chemical and behavioural aspects, with the multidisciplinary approach leading towards our better understanding of their significance. The development of new techniques, and the possibility for chemically analysing individual glands have recently led to new discoveries dealing with glandular ontogenesis and recognition systems, multicomponent signals and multiglandular involvement in the transmission of messages.

MORPHOLOGY OF EXOCRINE GLANDS IN SOCIAL INSECTS : AN UP-DATE 100 YEARS AFTER Ch. JANET

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The morphological information dealing with the exocrine system of social insects has known a major breakthrough with the magnificent descriptions by Auguste Forel in Switzerland in 1878 and especially by Charles Janet in France at the end of the last century. In spite of the inevitable problems dealing with making paraffin sections due to the intimate association of the exocrine glands with cuticular elements, Janet's work is characterized by an amazing accuracy. After the publication of these pioneer works, a long silent period in terms of morphological work followed until the development of new sectioning techniques using hard plastic embedding material for light microscopy, and the availability of a new research dimension with the electron microscope.

One century after Janet, our knowledge about the exocrine system in social insects deals with the existence of 63 different glands in total (39 when only considering the Formicidae, 21 for Apidae, 14 for Vespidae and 11 for Isoptera). In spite of this overwhelming variety, all these glands can be classified into one of two major types according to their cellular organization : *epithelial glands* (that represent a direct modification of the tegumental epidermis) and *glands formed by bicellular units*, each comprising a secretory cell and a duct cell (both originating from an epidermal mother cell through a complex process involving formation of a tetrad and subsequent degeneration of two of the four daughter cells). Both gland types, notwithstanding their different cellular organization, display very comparable ultrastructural features in relation to the elaboration of the secretory products. The glandular cells are generally characterized by a well developed Golgi apparatus and numerous mitochondria in addition to the presence of either smooth (the majority of pheromone producing glands) or granular endoplasmic reticulum (most venom glands and glands with a digestive function).

Because of their ubiquitous presence, the exocrine glands can be used in a phylogenetic context, as some are only found in particular taxa. In this way, the Formicidae share the unique but common presence of the postpharyngeal, metapleural and pygidial glands as neoformations. Unique for the social Apidae are the wax glands, while many social Vespidae are characterized by the presence of Van der Vecht's gland. Other glands, however, are only found in particular genera or species, their functions often still remaining unknown. The possibilities of today's embedding and sectioning techniques, together with the close association of the exocrine glands with cuticle, in the years to come very likely will reveal the existence of still more hitherto unknown glands among the social insects.

INTRA-NEST VARIATION IN EXOCRINE SECRETIONS OF COMMUNALLY NESTING BEES

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The majority of species of andrenid bees are solitary nesters whilst a small proportion show a low level of sociality, nesting communally. *Andrena jacobi* is a member of the latter group, widespread and common in Europe, and some of whose exocrine gland secretions have been well characterised by GC and GC-MS. Previous analyses of the chemical components of the Dufour's gland of this bee have been used to suggest that females who share a common nest entrance may be genetically related to one-another. We examine intra- versus inter-nest variation in exocrine secretions of provisioning *A. jacobi* females from 2 separated populations on the island of Öland, SE Sweden, and compare results with intra- and inter-population variation in exocrine secretions of other, solitary nesting, andrenid bee species. Chemical analyses combined with behavioural observations of *A. jacobi* female nest provisioning, pre- and post-reproductive dispersal suggest that relatedness amongst nest-sharing females of this species is low.

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THE GLANDULAR SOURCE AND THE MODE OF TRANSFER OF NESTMATE RECOGNITION CUES IN ANTS

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The postpharyngeal gland (PG) secretion of *Cataglyphis niger*, as in many ant species, is composed predominantly of long chain hydrocarbons. The congruency between this glandular hydrocarbons and those found on the cuticle suggests that they may play a role in nestmate recognition. This hypothesis was tested in a series of encounters between nestmates or alien ants that were either applied with a heterospecific PG secretion or left untreated. The aggression that is generally exhibited between two alien ants was significantly reduced if one ant was smeared with the PG's secretion of its contestant's nestmate. Similarly, an ant applied with a heterospecific PG's secretion was alienated by its nestmates. The behavior of the treated ants, on the other hand, was not modified in either of these tests. Analyses of the PG of members of mixed species groups of *Manica rubida* and *Formica selysi* showed the presence of the corresponding heterospecific hydrocarbons. This mutual exchange of hydrocarbons is apparently related to their ability to coexist in mixed species groups by creating a unified label. It further implies an active role of the PG in the transfer of recognition cues between nestmates. In order to test this hypothesis the incorporation of [¹⁴C] acetate into PG's and cuticular hydrocarbons and their subsequent transfer between nestmates was followed. Ants were injected with the radioactive precursor and 24 hrs later they were either sacrificed or encountered with a nestmate. The fate of the newly synthesized hydrocarbons was followed in intact or decapitated ants or in ants in which the mouth parts were blocked with bee wax. The hydrocarbons were extracted from the PG, the cuticle and from internal tissues and were further purified by TLC. These experiments revealed that hydrocarbons are synthesized by yet unspecified tissues that are associated with the cuticle, but accumulate in the PG. They are subsequently transferred between nestmates by trophallaxis independently of food transfer and reach the cuticle both by selfgrooming and allogrooming.

METAPLEURAL GLAND SECRETIONS IN ANTS

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Chemical analysis using gas chromatography and mass spectrometry of the metapleural glands of the Ponerinae : *Odontomachus bauri*, *O. chelifera*, *Hypoponera* sp., *Pachycondyla impressa*, *Ectatomma ruidum*, *Gnamptogenys tornata*, *G. striatula*, *Leptogenys* sp.1 and sp.2., Myrmicinae : *Zacryptocerus pussilus*, *Z. depressus*, *Daceton armigerum*, *Solenopsis geminata*, *Atta laevigata*, *Acromyrmex subterraneus*, *A. landolti*, *Trachymyrmex farinosus*, *Trachymyrmex* sp., *Mycetarotes parallelus* and *Sericomyrmex* sp., Pseudomyrmecinae : *Pseudomyrmex gracilis* and *P. termitarius*, Dolichoderinae : *Dolichoderus* sp., Formicinae : *Paratrechina longicornis* and Ecitoninae : *Eciton burchelli* revealed the presence of long chain acids and esters, among other compounds. *P. termitarius* and *Zacryptocerus* spp. lack a conspicuous metapleural gland and the specific secretions. The metapleural gland of most species is very similar, as they contain mainly hexadecanoic acid, octadecadienoic acid, oleic acid and octadecanoic acid ; although some species produce particular and distinct secretions which include the methyl and the ethyl-ester of 9-octadecenoic acid, 2-ethyl-5-tridecylpyrroline and others. From the known biological activity of some of the identified compounds, we confirm that the metapleural secretion in ants has mainly an antibiotic activity, with some exceptions such as perhaps *Solenopsis geminata*, where it may have a function as a territorial marker.

THE VENOM GLAND IN FORMICINE ANTS : AN ONTO-GENETIC AND ULTRASTRUCTURAL STUDY

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The primordia of the venom gland were found to occur in larvae starting from the third larval stage. In this developmental stage we observed imaginal discs. The venom gland primordium originates from larval abdominal segment VIII. The unpaired primordial venom gland develops during the fourth larval stage as a free-lying imaginal disc. In the fifth larval stage an open primordium was observed that already had undergone rotation. The most conspicuous changes in glandular development occur in the pharate pupa. The cells that form the convoluted gland form the internal cellular lining of the primordium. These cells invaginate towards the external cellular lining of the primordium and give rise to a group of cells that will form the convoluted gland filament and the free filament. The cuticular lining of all venom gland subunits is formed during the pupal stage. A remarkable aspect of the convoluted gland is that it originates in the primordium, whereas in adult ants it lies entirely on top of the reservoir. This is probably due to an enormous relative increase in length of the convoluted gland filament, so that its anatomical position in the early pupal stage inside the 'reservoir' cannot be maintained in the adult ant. The convoluted gland in adult ants is a single, in some species branched tubule provided with few secretory cells (units) that secrete into its lumen. The opening of the convoluted gland filament into the reservoir is situated near the reservoir apex.

When comparing the ontogenetic pattern described above with that in other ant subfamilies, it becomes clear that a fairly high degree of similarity exists for the early stages of glandular development.

The closing apparatus of the venom gland is also described in formicine ants. The gland duct often possesses two remarkable lateroventral cuticular processes. The median ventral portion of the duct is thickened for muscular attachment. A second set of muscles attaches to the lateral portion of the venom duct. A remarkable aspect is that one particular muscle attaching to the oblong plate, is involved in the closing apparatus of both Dufour and venom gland. Some specific staining techniques were used for demonstration of nerves innervating the glandular closing apparatus.

EXOCRINE GLANDS IN THE SOCIAL WASPS

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As in other social insects, exocrine glands play important roles in the social organization of wasps (Vespidae). This means that a full understanding of the mechanisms and evolution of social organization in this group cannot be achieved without a more complete knowledge of the roles of the secretions of these glands. Unfortunately our knowledge of the taxonomic distribution, functions, and chemistry of exocrine glands in wasps is extremely fragmentary. The purpose of this review is to summarize the state of our knowledge about gland function and to identify areas where research should be focussed. Glandular products in wasps include nest construction adhesives, venoms, alarm pheromones, sex pheromones, queen substances, nestmate recognition cues, trail pheromones, ant repellents, larval labial gland secretions, pupal thermoregulatory pheromones, and possibly antibiotic and brood food secretions. Some of these secretions serve to convey information while others are structural products vital to social life. In some cases we don't fully understand which function a particular gland product has. Is the labial gland secretion of the larva, for example, simply a nutrient for adults, or does it have a signal function, or both? Is venom an allomone? Exocrine products that function to convey information should be looked at from the standpoint of modern theory on communication and signal design. The taxonomic distribution of glands and their functions can be used to test phylogenetic theories about the evolution of such behavior as queen control, alarm-defense, and swarm founding. We cannot proceed very far toward an understanding of the evolution of queen control mechanisms without a knowledge of the pheromones and their primer and releaser effects. A comparative chemistry of exocrine secretions has not been attempted for any gland, yet has the potential to reveal much about the evolution of function. The main point to be made is that an increase in our rate of progress will come only if we move away from the current unsystematic, opportunistic approach to one that targets species or genera that stand at pivotal junctures in reconstructed phylogenies and proceeds apace on both behavioral and chemical fronts.

EXOCRINE SECRETIONS MEDIATING INDIVIDUAL AND COMMUNAL BEHAVIOUR IN TERMITES

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Termites have developed an efficient food recruitment scheme during which individual and communal behaviour is mainly mediated by chemical signals released from different exocrine glands. In the African termite *Schedorhinotermes lamanianus*, foraging for food is initiated by minor soldiers. By their sternal gland secretion they mark homing trails at low pheromon concentrations. Workers respond to trail-pheromon less sensitive than foraging soldiers and only follow pheromon trails which have been reinforced by frequent commuting of soldiers. When operating in the open, workers thus are always guided and flanked by soldiers. Predators intruding termite foraging parties are confronted firstly by soldiers, who release frontal gland secretion during combat. The frontal gland secretion not only elicits alarm behaviour in soldiers but also inhibits trail-following behaviour at concentrations of sternal gland secretion near threshold. Such concentrations are typical for foraging trails in the open. Termite workers consequently do not leave the protecting galleries during combat. In undisturbed situations, workers are led to newly discovered food sources by minor soldiers. Food recruitment starts when the first scout returns to the termite nest and lays a recruitment trail by its sternal gland secretion. Minor soldiers on their own are not able to elicit mass recruitment. Mass recruitment leads to communal exploitation of the food source. During the initial period of food exploitation, *S. lamanianus* workers release labial gland secretion, which leads to aggregations of workers at gnawing sites and thus to a highly contagious pattern of compact colonies of workers. During the enhanced exploitation of a food source, aggregations of workers accumulate and finally merge. Despite of this development distinct areas of the food source remain free from gnawers and serve as commuting zones. Sternal gland secretion inhibits dose-dependent the formation of gnawing aggregations and resolves already existing aggregations. The disintegration of the foraging area into feeding zones and zones for commutation is regulated by the balance between labial gland secretion and sternal gland secretion.

DEFENSIVE SECRETION OF *NASUTITERMES* SOLDIERS : VARIATION IN THE COMPOSITION, CHIRALITY OF MONOTERPENES

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Specific chemicals are involved in various phases of the termite life. Mono- and diterpenic compounds are found in the frontal gland secretions of *Nasutitermes* soldiers. Their function as alarm pheromones as well as defence substances has been shown earlier.

Five *Nasutitermes* species were studied, including several colonies within each species. The compositions of their secretions varied to different extent in different species. *N. costalis* showed a low variation between colonies both in diterpenes and monoterpenes, including their enantiopurities. In *N. ephratae*, great differences in the content of monoterpenes were found between colonies, while the proportions of diterpenes were similar in all samples. *N. nigriceps* and *N. rippertii* differed widely in all chemical aspects - the content of diterpenes, monoterpenes and their enantiomeric compositions. As regards the chirality of monoterpenes, 3-carene, β -pinene and β -phellandrene were present in a high enantiopurity in most of the samples, while α -pinene, limonene, and camphene showed a great variation between individual termite colonies. Pure (-)-3-carene was found in *N. costalis* and *N. ephratae* termites. This is in contrast to the situation in plants, where pure (+)-enantiomer is present in most of the material. Possible biosynthetic correlations between monoterpenes in termites and plants will be discussed.

ECOLOGICAL IMPORTANCE OF CUTICULAR HYDROCARBONS SECRETED FROM THE TARSUS OF ANTS

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During the cooperation to the production of the movie "Rhapsody in August" directed by Akira Kurosawa, we found that the ant *Lasius fuliginosus* that followed the trail pheromone had to secrete some kind of anti-absorbant when it laid the trail.

When the ants walked on the petri dish, they left a large amount of lipid on the glass surface. The same result was also found for *L. niger* that also lays a trail. Those footprint lipids consisted of colony-specific hydrocarbons and the pattern just resembled the colony-specific cuticular hydrocarbons. Both of the ant species recognized the difference of the HPs on which they walked. These results indicate that hydrocarbons secreted from the ant tarsus fulfils two functions as anti-absorbant and territory marking pheromone.

The trail pheromone of *L. niger* is not colony-specific but the ant prefers the trail laid route on a paper precoated by foot print hydrocarbon (FPH) of the same colony members. The FPH of *L. niger* consists of n-alkane, branched alkane, alkene and alkadiene. We could check the ant preference to the precoated line treated by artificial blended FPHs. The ant was very sensitive to the change of branched alkane and unsaturated alkene profiles. But the ant could not recognize even the big change of n-alkane. The results may indicate that n-alkane does not work as a signal in colony odor. By this precoated method we will be able to determine the relative importance of each hydrocarbon in nestmate recognition using synthetic components.

All of the ants analyzed left FPHs on a glass. So this gradual change of FPH density on the ground around the nest site may act as a chemical signal for the ants who do not use trail pheromone but can come back to the nest.

FIRST IDENTIFICATION OF A PHEROMONE OF AN ARMY ANT: THE TWO-COMPONENT TRAIL PHEROMONE OF *AENICTUS* SPECIES.

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The periodic raiding and foraging behaviour of the Old World army ants (subfamily Dorylinae) has been well documented, but essentially nothing has been known about how these raiding columns of totally blind ants were directed. Although the sources of some pheromones have been located in certain glands, no pheromones of this subfamily have been identified chemically. The existence of a trail pheromone in a (probably new) species of *Aenictus* close to *A. laticeps* has been demonstrated. The source of the pheromone is the postpygidial gland. The pheromone consists of two parts, a primer and a releaser component. The workers are unable to follow either component alone, but when suitably primed, they were able to follow the releaser component to exhaustion. The primer component could be mixed with the releaser or administered up to several hours before the releaser to induce trail-following when the second component was laid down. The primer substance has been identified as methyl nicotinate and the releaser component is methyl anthranilate (methyl 2-aminobenzoate). Suitable mixtures of the synthetic substances completely reproduce the behaviour released by a single worker postpygidial gland in laboratory tests.

SELF SACRIFICE IN *GLOBITERMES SULPHUREUS* HAVILAND SOLDIERS : FRONTAL GLAND DEHISCENCE

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When attacking, the soldiers of *Globitermes sulphureus* Haviland may rupture their abdomen, spraying defensive fluid which often entangles both termites and enemies (Bathellier, 1927). This suicidal behavior was the first example of defence by self-rupturing or autothysis. *G. sulphureus* is a very common economically important termite species in Southeast Asia, that builds a protective epigeous dome-like nest with a complex internal architecture (Noirot, 1959). Soldiers with elongate curved mandibles of the slashing type are characterized by the yellow colour of their abdomen which is due to the accumulation of the defensive secretion in an impair and dorsal gland occupying the thorax and a great part of the abdomen. This gland does not enter into the head capsule and does not open outside. In the thorax, it shows a horse-saddle shape with lateral expansions reaching the sternal wall where the secretion flows out after the rupture of the arthrodial membrane, just behind the forecoxae. No relation was observed between this gland and the normally developed salivary gland reservoirs filled with hyaline liquid and opening into the buccal cavity. The monolayered epithelium of the defensive soldier gland is composed of 5-10 μm thick class 1 cells. No cuticular intima is recognizable. Presoldiers possess a frontal spherical gland (200 μm in diameter) with thick glandular epithelium (20-25 μm) located in front of the cephalic capsule. There is no frontal pore, but some cells observed on histological sections could represent a vestigial canal. At the end of the presoldier stage, when soldier morphogenesis is occurring, the presoldier frontal vesicle transforms into a large reservoir which moves into the thorax and the abdomen. These observations show that the defensive gland of *G. sulphureus* soldiers is a very transformed frontal gland and not the salivary gland reservoirs as previously reported (Bathellier, 1927). Thus, *Serritermes serrifer* (Serritermitidae) (Costa-Leonardo and Kityama, 1991) and *G. sulphureus* (Termitidae, termitinae) are the only known examples of autothysis by frontal gland dehiscence in termites.

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SYMPOSIUM «INSECT COLONIES: ADAPTIVE DESIGNS AND AUTO-ORGANIZATION»

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Human technological achievements are truly remarkable. We can build cathedrals, jumbo jets, and computers that are true marvels of complexity. The rules for building such structures or machines are themselves complex. The how-to manual for building a 747 no doubt would contain tens of thousands of pages. Someone - the architect or computer designer - has to put together the blueprint for these things, and the behavior behind it requires many years of training and can be described as complex by any measure. We feel certain that we can do these things primarily by virtue of our brain power.

Surely the behavior of the individuals that construct something as large and structured as a *Macrotermes* nest or that organize a group foraging effort so as to optimize exploitation of resources according to their cost/benefit ratios must be similarly complex. But how can that be, given that the brain of a bee or an ant has only a few hundred thousand neurons - 5 or 6 orders of magnitude fewer than we have ? How can natural selection, working on organisms with brains no bigger than motes, produce such complex output at the group level ? Oddly, it is beginning to appear that complex behavior such as we see being carried out by colonies of social insects actually require only rather simple behavior patterns in the individual workers within the colony. The complex colony-level behavior almost seems to be an epiphenomenon, an property emerging through rather fundamental laws of self-organization.

The effort to understand social insect behavior in this light is not new. An early effort was the work of Grassé here in France with building behavior in termites, leading to the concept of «stigmergy». Nor is this the first symposium to address the issue. A workshop held in France in 1986 had as its title, «From individual to collective behavior in social insects». Inspired by Ilya Prigogine and organized by Jacques Pasteels and Jean-Louis Deneubourg, all of Belgium, its participants discussed early efforts along these lines. So in a sense we are meeting at the «epicenter» of the discipline and we are grateful for this opportunity to come together to learn firsthand of each other's latest thinking on the topic. Because this is still a young subdiscipline of insect sociobiology, there are a variety of approaches to the problem.

The problem of understanding colony-level behavior focuses our attention on the properties of two different levels of biological organization and how they are related. Looking at individual workers, we can ask what behavioral rules at the individual

level lead to the behavior that we observe at the colony level. If the rules are simple, does this mean that the workers themselves are simple ? Or do they require complex abilities in order to follow simple rules ? At the colony level, our first problem is how to describe the behavior formally, even quantitatively. Such descriptions are needed for rigorously testing whether a given set of individual rules can actually explain the colony behavior. Once we are able to explain how colony behavior arises from individual actions, we would like to identify adaptive features of the behavior and ask how they have evolved. To do this requires that we be able to perceive the dynamic behavior of colonies in the same way we view the morphology of animals, to be able to see regularities in the patterns of worker movements through time and space.

It is appropriate to begin the symposium with an understanding of terms, and this is what Camazine and Deneubourg tackle in their opening presentation. They define self-organization as the occurrence of patterns in space and/or time produced at the system level by virtue of interactions among system components. Camazine and Deneubourg show how a system governed by a few simple rules involving positive and negative feedback can suddenly create an orderly structure at the global level. They go on to demonstrate by example that systems differing in their structure may employ similar mechanisms and that self-organization allows natural selection to economize on the complexity of individual behavioral rules.

In the second paper, the same authors address the question of just how much individual complexity is required to produce the observed global complexity. They draw on examples of building by ants to show how some of these rules work to create complex behavior. They also show the role of amplification of environmental heterogeneities, of physical constraints, and of information obtained from cues to modify collective decisions.

Karsai and Péntzes then describe their work with building in *Polistes dominulus*. Based on observations and computer simulations, they have developed a simple algorithm in which in building contributions of individuals, each behaving according to very simple rules and responding largely to local feedback from the nest structure, can lead to the construction of the regular combs built by these wasps.

Jeanne, also addressing the social wasps, argues that the two groups of polistine wasps, the independent founders and the swarm founders, show different patterns of colony organization. In the first group, exemplified by *Polistes*, colony activity is regulated largely by the queen, while in the swarm founders much of this role seems to be shifted onto the workers. Other behavioral traits characterize each group, suggesting that the two reflect fundamentally different ways of achieving complexity at the colony level.

According to previous work by Jaffé's group, recruiting ants have either a «democratic» decision-making system or an «autocratic» one, and the occurrence of these two types is correlated with the degree of stability of the resource being exploited. In their contribution to this symposium, Issa and Jaffé tell us what they find when they extend their work to two termite species in the genus *Nasutitermes*.

In the final paper of the morning session, we continue with the subject of recruitment, but return to the ants. Earlier work, primarily with mass-foraging species, has suggested that colonies consisting of numerous individuals, each with rather simple behavioral repertoires, can generate complex behavior at the colony-level. Robson and Traniello, working with a group-retrieving ant, show that individuals are not interchangeable, but that a foraging party has a structure to it. In short, individual behavioral repertoires in this species are not at all simple.

In the afternoon we start off with a paper that takes a somewhat broader look at ant behavior. How do ant colonies allocate workers to a variety of tasks, including foraging? Deborah Gordon has done extensive empirical work on this subject and is now using this to develop theoretical models. She gives us two, both of which see task allocation as a distributed process in which individuals decide what to do based in part on their rate of encounters with other workers. Not only that, but her models show how colony size influences the outcome.

The next paper continues in a similar vein, and adds into the mix a phenomenon that will be a focus of the remaining talks of the afternoon session, namely age polyethism. We know that age polyethism is a nearly universal characteristic of social insect colonies. How rigidly does the age distribution of the individuals in an ant colony dictate the relative effort a colony allocates to various tasks? Not very rigidly at all, argues Beshers. His studies on fungus gardening ants suggest that colony size and need are much more important.

We next turn our attention to honey bees, and to the physiological underpinnings of age polyethism. We know that age polyethism is plastic, that what tasks a bee of a given age will perform can be altered by manipulating the relative needs of the colony and, further, that the titer of juvenile hormone, or JH, in a bee in manipulated colonies follows its behavior rather than its age. Huang and Robinson now present evidence that JH level and task are not so rigidly correlated, but that if task is held constant, JH level varies with season, suggesting that the role of JH in division of labor is more complicated than previously suspected.

Theraulaz and colleagues add yet another parameter, namely learning, to the mix of factors influencing colony organization. They present a theoretical model that shows how individual learning interacts with the asynchronous birth of new workers and the spatial sorting of the brood within the nest to produce the observed correlation between age and task.

The final paper hits us with a provocative question: «Is age polyethism a myth?». Having got our attention, Franks makes his case for his «foraging for work» model, which shows that task allocation works best if individuals are not hard-wired to perform certain tasks at certain ages. Is age polyethism then just an epiphenomenon of more fundamental forces at work?

WHAT IS SELF-ORGANIZATION?

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Self-organization is a recent approach to understanding pattern formation in colonies of social insects. With the novelty of the approach comes inevitable misunderstandings about what self-organization is and how it works. We propose the following definition: Self-organization is a mechanism for building pattern at the global (collective) level by means of multiple interactions among components at the individual level. The components interact through local, often simple, rules that do not directly, explicitly code for the pattern. By pattern, we mean a definite arrangement of parts in space, or in time, or both. Examples of pattern include the formation of army ant trails, the distribution of bees at an array of food sources, the characteristic pattern of honey, pollen and brood on honey bee combs, or the rhythmic activity cycles in an ant colony. Self-organizing systems typically involve a large number of components. Often, these components are the individuals in a group, such as a cluster of bees collectively regulating the temperature of their swarm. The components may also be inanimate objects, such as bits of soil used by termites in the construction of a their mound. These components interact in particular ways. Positive feedback, in the form of a few simple behavioral rules, is a powerful mode of interaction that provides a mechanism for creating pattern and structure. But without an antagonizing mechanism, negative feedback, the process can snowball. Positive and negative feedback can be provided by behaviors based upon information that an individual acquires from other individuals, from itself, or from the environment. In addition, the environment often provides negative feedback in the form of physical constraints. A system governed by these rules of interaction may suddenly break out of an "amorphous" state and become an orderly structure. This talk presents several examples of self-organization in insect societies in order to emphasize two points: (1) That widely different systems employ similar mechanisms, and (2) That self-organization allows natural selection to economize on the complexity of individual behavioral rules.

HOW THE ENVIRONMENT CAN SIMPLIFY THE BEHAVIORAL ALGORITHMS OF SOCIAL INSECTS

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A key problem in the study of social insects is to establish a link between individual behavior and global structures. Of particular interest is the question of how much individual complexity is required to produce the observed global complexity. In many cases, self-organization can provide a powerful mechanism for generating collective structures. An important feature of these self-organizing systems is that natural selection often produces simple behavioral algorithms that allow social insects to exploit physical constraints in the environment. Individual behaviors modify the environment, feeding back on individual behaviors, resulting in complex global structures. This is not a new idea but today it appears that these mechanisms are more powerful than we imagined. In fact, we find similar strategies among many different social insect activities. Using examples of building by ants, involving the piling and clustering of materials, we discuss: (1) How collective decisions arise through amplification of environmental heterogeneities, (2) How physical constraints, such as available space, affect global patterns without the need to modulate individual behaviors, (3) How, in other cases, insects modulate their behaviors and communication by exploiting simple, information-rich cues. In these self-organizing systems, the interplay between positive and negative feedbacks provides the driving force for structure formation. Often, individual behaviors code for positive feedback and the environment provides negative feedback. The inverse situation is also observed, in which the environment provides positive feedback (leading to complexity) and individual behaviors code for negative feedback (leading to a simplification and regularity of the structure).

ROUND COMBS IN WASPS: ARE THE WASPS AWARE OF WHAT THEY BUILD?

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From the point of view of behavioural ecology, the round wasp nests provide nice examples of the adaptiveness of the structures that are molded by the economic usage of material. Contrary to the studies of function, we have very limited knowledge about how wasps build these regular structures. A building script of *Polistes dominulus* based on a kind of self-organization is presented.

Observations on building behaviour of individuals revealed that constraints stem from the structure itself and the mutual dependence between these constraints and the building postures performed by the wasps. As the nest develops, spatial constraints become more subtle and the nest provides more and more stimuli both in number and kind. The structure emerges from this dynamic stimulus-reaction process.

Computer simulations demonstrate that the wasps are able to construct the round shape combs using only local information which comes from the cell below the head of the wasp. Memory and direct communication amongst the builders were not necessary to construct a regular structure. Indirect communication through the construction seems to be sufficient to organize the work in the social milieu and govern the growing process of the nest.

Analyses of nest forms, which were produced by wasps and different building algorithms predicted two possible ways of optimization: 1, minimal material usage; 2, maximal compact cell arrangement. These kind of optimizations should require global information from the structure. A proposed simple algorithm, which uses only local information is able to produce the optimal comb forms and make the same errors as the wasps. In this case, a simple builder's rule of thumb results in a quasi-optimal solution.

We believe that simple animals like wasps with very limited intelligence are able to construct very regular nests without awareness of the global properties of the structure. Simple behavioural rules based on local cues and indirect communication through the structure is sufficient to organize the builders and to regulate the building process.

PATTERNS OF COLONY ORGANIZATION WITHIN THE VESPIDAE

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The independent-founding Polistinae (IF) were originally characterized (Jeanne 1980) as founding colonies by one or several queens working without the aid of workers; reproductive dominance is based on direct physical attacks by the queen. In the swarm-founding Polistinae (SF), colony founding is by a swarm of workers accompanying several or many queens (polygyny); reproductive dominance involves pheromones. The Vespinae form a third group, similar to IF in their haplometrotic colony founding, but having at least some pheromonal involvement in reproductive dominance (Jeanne 1980). In *Polistes*, colony activity is controlled largely by the queen, who directly incites her subordinates to work (Reeve 1991). In the SF, in contrast, much of the regulation of worker activity seems to be shifted onto the workers themselves; queens are relatively passive. The Vespinae are instructive in demonstrating that a single species can manifest either an IF- or an SF-like mode of organization, depending on circumstances. There is evidence that the two groups also have different forms of colony productivity curves: curves of per capita productivity decline in the IF as group size increases, while in SF they increase (Jeanne, in prep.). Some IF genera, notably *Ropalidia*, show SF-like traits, such as the coexistence of several egg-layers and the absence of overt dominance by the queen. Nevertheless, there appears to be a discontinuity, or "adaptive valley," between the IF and the SF modes, in which intermediate stages are apparently lacking and may be evolutionarily unstable.

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DECISION-MAKING SYSTEMS IN RECRUITMENT TO FOOD IN TERMITES

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The models proposed by Jaffe et al (1985) regarding the decision-making systems used by ant societies for recruitment, predict that ants use democratic systems (the trail used is the result of the addition of individual trails) when concentrated but peremptory resources are exploited. On the other hand in the autocratic system (few trails of certain individuals form the trail used by the colony) is preferred by species that exploit stable resources in time and space. The object of this work is to determine the decision-making mechanism used by the termite *Nasutitermes corniger* and *N. ephratae*, (Termitidae:Nasutitermitinae). Our results reveal that both species show an autocratic decision-making system as is evidenced by an unchanged rate of recruitment (in the fast recruitment phase) for different distances between an active trail and a new food source (2,10 and 50 cm for *N. corniger* and 2 and 15 cm for *N. ephratae*). Furthermore, no significant differences were found in the fast phase of recruitment when large and small nests of *N. corniger* were used with fixed distance between an active trail and a new food source. This is in contrast with what was reported by Verhaeghe and Deneubourg (1983) for the ant *Tetramorium impurum*.

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COOPERATIVE PREY RETRIEVAL IN *FORMICA SCHAUFUSSI* (FORMICIDAE): GROUP BEHAVIOR BASED ON INDIVIDUAL COMPLEXITY RATHER THAN SIMPLICITY

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Many studies have examined the relationship between colony design and foraging in ants, exploring how adaptive colony-level behavior can arise through the collective action of relatively simple individuals (Wilson 1962, Deneubourg & Goss 1989, Traniello & Robson in press). A colony design based on numerous simple, redundant individuals is considered to maximize overall system flexibility and reliability. However, this approach has been applied to predominantly mass-recruiting species. Examining the organization of foraging in the group retrieving ant *Formica schaufussi* with a protocol that emphasizes descriptions of both individual and group behavior provided insight into the generality of the 'complexity from simplicity' model of social insect behavior. In contrast to mass-recruiting ants, individuals involved in prey retrieval display a high degree of behavioral complexity, context-specific behaviors and lack interchangeability with other workers. Components of individual behavior (residency time at the prey, the probability of recruiting new individuals to the prey) are a function of the stage at which an individual enters the recruitment process (discovering versus recruited ants) and the presence of the discovering ant is required to maintain group cohesion and successful retrieval. The removal of the discovering ant during the process of recruitment leads to the dissolution of the retrieval group. Group action can therefore result from the behavior of workers with a complex behavioral repertoire.

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INTERACTION RATES AND THE EVOLUTION OF TASK ALLOCATION

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A social insect colony performs a variety of tasks. Recent empirical studies show how colonies alter the allocation of workers to different tasks, depending on environmental conditions. How does task allocation operate? Answering this involves understanding how relatively simple individual decisions lead to colony-level patterns in numbers of individuals performing each task. Individuals decide whether to be active and whether to switch tasks. Task allocation operates differently in large and small colonies. What cues do individuals use to decide whether to be active and which task to perform, and how does colony size affect these decisions? One possibility is that individuals use the rate at which they encounter others as a cue. Recent studies of the ants *Lasius fuliginosus*, *Linepithema* (= *Iridomyrmex*) *humile*, and others, show that ants respond to changes in encounter rate, and that individuals adjust their movement patterns in response to numbers of other individuals participating in certain tasks. Two models of task allocation as a distributed process will be presented. In both models, individual decisions are based in part on the rate of encounter among individuals. These models suggest how task allocation depends on colony size. Much empirical work remains before we understand how individual behavior generates task allocation at the colony level. When this is achieved, it will be possible to investigate the evolution of task allocation. If task performance is important for colony fitness, then natural selection should act on the processes that determine how much of each task is accomplished. Eventually we hope to learn how variation among colonies in the ways they respond to environmental conditions is related to variation among colonies in reproductive success.

ADAPTIVE DESIGN IN *TRACHYMYRMEX SEPTENTRIONALIS*: COLONY-LEVEL BEHAVIORAL TRAITS

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Caste theory states that division of labor in social insects evolved to increase colony efficiency, mainly by taking advantage of variation in individual traits that affect task performance (Oster and Wilson 1978). Recently there has been increasing emphasis on the organization of colonies, and how that organization affects colony-level performance. Age polyethism has common features in most social Hymenoptera, suggesting that this system has features essential to colony operations (Beshers and Traniello, submitted). Two aspects of colony organization were studied in the fungus gardening ant *Trachymyrmex septentrionalis*. Allocation of workers among the roles of fungus tending, brood care, substrate preparation, nest maintenance and foraging was studied by observing individually marked workers to determine the number devoted to each role. These patterns were analyzed in relation to colony size, age composition, and quantifiable colony needs such as number of larvae and the size of the fungus comb. Variation in the degree of task specialization and in activity level, or rate of task performance, were studied by compiling repertoires for individual workers based on more than twenty hours of observation. Allocation was determined by colony size and needs, but within broad limits was not affected by the age distribution of the workers. Individual specialization and activity levels were highly variable, but appeared to exhibit characteristic profiles for each role. These studies suggest that there are stable and predictable patterns of colony-level behavior that do not depend on the intrinsic characteristics of individual workers and are not explained by current models of age polyethism. These colony-level behavioral traits may shape colony responses to transient changes in task needs.

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SEASONAL CHANGES IN JUVENILE HORMONE LEVELS IN WORKER HONEY BEES (*APIS MELLIFERA*)

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Age polyethism in worker honey bees is regulated by juvenile hormone (JH). Three forms of plasticity in age polyethism have been shown: accelerated behavioral development (i.e., premature foraging), with a premature rise in JH titers; delayed behavioral development (overage nursing), with a delayed rise in JH titers; and reversed behavioral development (from foraging to nursing), with a drop in JH titers. In most studies these forms of endocrine plasticity have been induced experimentally. We report seasonally related endocrine plasticity: hormonal reversion, the decrease of JH in workers with previously high levels, under natural conditions. Foragers showed a significant decrease in JH rates of biosynthesis and titers over the course of the fall. Under our experimental conditions foragers did not survive the winter. Newly emerged bees in the early fall also showed a similar decrease; they did survive the winter and then showed an increase in JH in the spring (as in Fluri et al. 1982). Similar hormonal reversion also was induced experimentally. Relocating a colony into an indoor environmental chamber (4°C) in the summer caused a significant decrease in both worker JH titers and rates of biosynthesis. These results demonstrate plasticity in endocrine development under natural conditions. They also suggest that seasonal changes in JH are related either to seasonal changes in temperature or seasonal changes in colony social structure that affect endocrine and behavioral development (see Huang and Robinson, 1992), or both. We also found that foragers in the late fall and early spring had low levels of JH, while they were foraging. The JH levels of foragers gradually increased from spring to summer. The occurrence of bees that forage with low JH levels has not been detected during the summer months. These results suggest that the role of JH in division of labor is more complex than previously suggested.

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NEST SPACE STRUCTURATION COUPLED WITH INDIVIDUAL LEARNING PRODUCE AGE POLYETHISM IN ANT COLONIES

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We present a theoretical model which accounts for the genesis of age polyethism in ants colonies. Previous experiments have shown that ants not only structure their environment (e.g.: the brood is sorted in different categories of items over the nest space), but use this primary pattern to organise themselves, *i.e.* to differentiate themselves into specialized roles associated with particular classes of brood stimuli. In our model, the interaction between learning at the individual level, asynchrony in the birth of new workers and the space differentiation due to the continuous activity of the colony is able to reproduce a correlation between age and division of labor. Then, it is possible to produce a link between the age of an individual, the task it carries out and its location in space, even if such relations are not preprogrammed at the level of each individual.

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IS AGE POLYETHISM A MYTH ?

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One of the most widespread concepts in studies of social insect behaviour is that age polyethism is fundamental to the division of labour. The non-trivial definition of age polyethism is that there is a causal relationship between age and task allocation. Recently, Tofts and Franks (1992) (see also Tofts 1993, Franks and Tofts 1994) have suggested that the (weak) correlation between age and task that is observed almost universally in social insects, may arise due to the spatial structure of tasks in nests, to the system of employment seeking and task switching and to workers first becoming adults at the centre of the nest. Their model known as the foraging for work algorithm shows that an association between age and task does not necessarily imply a relationship of cause and effect. The foraging for work algorithm suggests that task allocation may be maximally flexible if individuals are not hard-wired to perform certain tasks at certain ages. Foraging for work can still operate effectively if certain propensities to task switching change with age. But this would imply only that ageing may have some influence, not that the division of labour is age based. This paper considers both these empirical and theoretical issues and suggests (a) that age polyethism can no longer be assumed a priori and (b) that temporal polyethism is a less prejudicial and is therefore a much more appropriate term.

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INTRACOLONIAL CONFLICTS 2. PROXIMATE FACTORS

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At a proximate level, the resolution of reproductive disagreements in colonies of eusocial hymenopterans is based on direct interference. Intracolony attacks are observed in some bees, wasps, lepto thoracine and ponerine ants, whereas in many other species sterility of the majority of nestmates is maintained by mechanisms other than aggression (probably pheromone-based). These alternative modes of regulation may be interpreted as an evolutionary continuum. When dominance hierarchies are established, aggressive interactions (sometimes including oophagy) and the resulting endocrine differentiation function to suppress oogenesis in subordinate individuals. Pheromonal signals are probably also important to recognize higher-ranked individuals, because attacks stop once hierarchies have become stable.

Dominance hierarchies can involve different types of participants: i) monomorphic females, e.g. in primitively eusocial wasps and bees; ii) morphologically specialized queens, e.g. in many functionally monogynous, as well as polygynous, ants; iii) members of the worker caste, e.g. in queenless ponerine ants (where mated workers produce all diploid progeny), or lepto thoracines (where virgin workers produce males in the presence of the queen). In each case, protagonists exhibit few or no differences in phenotype, and also they are not numerous (colonies are small). In contrast, dominance interactions are less likely between members of distinct castes, especially when these differ in fighting ability. In species with two morphological castes, workers lack reproductive specialization and are more likely to forego direct reproduction whenever they detect the presence of a queen. If queen control and queen recognition are to be distinguished (West-Eberhard 1977), the effect of pheromones on the ovarian activity of subordinates/workers must be experimentally investigated.

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COLONY CONFLICTS AND THE ROLE OF PHEROMONES

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The theoretical expectation of queen-worker conflict and observed effects from removing queens has led to the concept of "queen control", which can be defined as workers or subordinate queens being manipulated by a dominant queen into pursuing actions that are contrary to their inclusive fitness. In large colonies, manipulation of workers by queens has been proposed to occur through "pheromonal queen control" whereby chemicals exuded by the queen(s) replace physical intimidation in forcing workers to behave in ways that increase queen fitness. We will argue, however, that pheromonal queen control has never conclusively been demonstrated and is evolutionarily difficult to justify (see also Keller and Nonacs 1993). Proposed examples of pheromonal control are more likely to be honest signals, with workers' responses increasing their own inclusive fitness.

Keller, L. and Nonacs, P. 1992. The role of queen pheromones in social insects: queen control or queen signal? *Anim. Behav.*, 45, 787-794.

CONFLICT AND REPRODUCTIVE SKEW AMONG QUEENS IN LEPTOTHORAX ANTS

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Societies of ants with multiple queens represent valuable study systems in which to investigate the evolution of a stable reproductive skew (allocation of reproduction). The leptothoracine ants are particularly interesting in this respect because some species are functionally monogynous (only one of several mated queens lays eggs at any one time) and others are facultatively polygynous (with multiple egg-laying queens). Why in the same group should there be societies with high skew (functional monogyny) and low skew (facultative polygyny)? This presentation has two aims. First, I describe work with the facultatively polygynous ant *Leptothorax acervorum* to measure skew. Methods include observations of egg-laying and egg-cannibalism rates, allozyme analysis (in collaboration with Dr Jürgen Heinze, University of Würzburg), and the analysis of parentage using hypervariable microsatellite loci (in collaboration with Dr Mike Bruford and Harriet Green, Institute of Zoology). Second, using arguments developed with Dr Jürgen Heinze, I propose that the stable skew models of Reeve and Ratnieks (1993) provide a good explanation for high and low skew leptothoracine societies. These models also help explain why functionally monogynous societies are associated with patchy habitats and high within-colony aggression. Similarly, they account for why facultative polygyny is associated with uniform habitats and low aggression. The conclusion is that these models help explain much of the social and ecological diversity observed in leptothoracines (Bourke and Heinze 1994).

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DOMINANCE BEHAVIOUR AND THE RESOLUTION OF INTRA-COLONIAL CONFLICTS IN THE PRIMITIVELY EUSOCIAL WASP, *ROPALIDIA MARGINATA*

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Ropalidia marginata is a primitively eusocial polistine wasp restricted to the old world tropics and sub-tropics. New colonies are initiated by one or a group of wasps throughout the year. During colony initiation, strong dominance-subordinate relationships, characteristic of polistine wasps are the means by which one individual establishes herself as the sole reproductive, while the others serve as workers. By about the time of the hatching of the eggs into larvae and throughout the colony cycle from then on (except during queen replacements), dominance behaviour appears to take on a rather different meaning. Firstly, dominance behaviours are now restricted to only a milder subset of the repertoire seen during colony initiation. Secondly, most of the dominance behaviour is shown by the workers while the queen, who continues to enjoy exclusive reproductive rights becomes a rather quiet individual and shows little dominance behaviour or any other kind of behavioral interaction with the workers. Loss or experimental removal of the queen at this stage makes no difference to worker activity levels, including, foraging, bringing food and feeding larvae but it results in one individual among the workers becoming extremely aggressive and dominant. This "potential queen" goes on to become the next queen if the original queen does not return. There is good evidence that in such established colonies, workers regulate their own levels of activity through a process of mutual interaction and the queen merely regulates worker reproduction, not by any overt behavioural means but perhaps by a chemical means. Thus, intra-colony conflicts with reference to reproductive division of labour appear to be resolved by apparently different proximate mechanisms during colony founding as compared to in well established colonies and also differently with reference to reproductive division of labour and worker activity regulation in established colonies.

DOMINANCE HIERARCHIES AND GAMERGATE DIFFERENTIATION IN QUEENLESS PONERINE ANTS

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In ponerine ants without morphologically specialized queens, reproductive differentiation among the workers is achieved through physical confrontations. Colonies are typically small (less than a few hundred individuals), and only a proportion of nestmates are involved. This intracolony aggression leads to the inhibition of ovarian activity in subordinates, and sometimes it regulates mating as well (all workers have a spermatheca). The dominance hierarchies reported in Ponerinae are extremely diverse in their characteristics, which is not surprising since gamergate reproduction has evolved independently in various genera belonging to all four tribes. The nature of aggressive interactions (biting or ritualized antennal boxing; oophagy or not) varies widely between species. Size of workers has never been shown to be associated with dominance ranks, but age is often crucial. The occurrence of monogyny or polygyny (Peeters 1993) has a major influence on the pattern of hierarchy formation. Once a hierarchy is established in orphaned colonies of *Diacamma vagans*, only the top-ranking worker will produce eggs, and only she will mate when foreign males visit the nests. In contrast, many young workers mate annually in *Harpegnathos saltator*, but most of them will not oviposit as a result of dominance interactions. In stable colonies of *H. saltator*, several gamergates monopolize reproduction, and coexist peacefully; however they are often closely investigated by some callow workers.

Outstanding problems in the investigation of dominance hierarchies include: (i) is short-term individual recognition possible during hierarchy formation?; (ii) are chemical cues associated with oogenesis used for recognition of potential competitors?; (iii) how do subordinates recognize higher-ranked workers? (aggression stops once hierarchies are stable, but resumes quickly following removal of dominants); (iv) in polygynous species, is there reproductive skew among the gamergates? Data on the mechanisms of hierarchy formation are usually obtained by experimental manipulation, but little is known about the natural replacement of one cohort of gamergates by another (e.g. following mating activity). Better techniques of data analysis and presentation are needed to study changes in dominance over time. The absence of intracolony aggression has been noted in a few queenless ponerines, but further research needs to determine whether this is also the case during hierarchy formation.

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THE SELF-ORGANIZATION OF HIERARCHICAL STRUCTURE IN THE PRIMITIVELY EUSOCIAL WASP *POLISTES DOMINULUS* (CHRIST)

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We studied the genesis of hierarchical structure in colonies of the primitively eusocial species *Polistes dominulus* in order to determine very precisely the behavioral processes involved in the hierarchical differentiation of the individuals. Observations revealed a highly inhomogeneous participation of individuals in these interactions. In particular, the dominance index, associated with the hierarchical rank of each individual, is not a *linearly* decreasing function of the rank. Similar results were also described in ants. It is the variation of the probability of interaction according to the rank which results in this heterogeneity: the probability of interaction decreases exponentially with rank. One possible mechanism involved in the genesis of the hierarchy, is a kind of learning or positive feedback. As wasps move around the nest, the encounters between pairs of individuals occur more or less randomly, and each animal reinforces its probability of dominating through the number of times it is successful in hierarchical interactions; each subordination has the opposite effect. We present different models based on these processes and analyse in each case how critical parameters — the individual recognition, the rates of learning and forgetting and the size of the colony— can shape different hierarchical structures with different adaptive values. We show that such processes not only enable the genesis of different types of stable hierarchical structures which closely match those found in different wasp species, but allow for the re-establishment of this structure when it has been destroyed previously. Hierarchy was found to distribute the individuals of the colony over the nest space. Wasps are gradually excluded from the nest according to their rank and learning associated with brood rearing and foraging tasks produced a more indirect competition between individuals through the level of nutritional status of the larval brood and leads to the division of labor.

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Fighting and thelytokous parthenogenesis in the ant, *Platythyrea punctata*

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Observations and experimental manipulations in three colonies of the ponerine *Platythyrea punctata* from Florida suggest that virgin workers compete aggressively for the production of diploid offspring from unfertilized eggs. Though none of the colonies contained a morphological queen when collected, for more than one year eggs and larvae were produced which developed into appr. 50 workers and one queen. Dissection of all 14 workers of one colony and additional 12 workers from other colonies showed that none was inseminated and that their spermathecae were only rudimentarily developed. From eggs laid by a group of workers, which had been removed from their maternal nest either as pupae or callows and thus definitively had not mated, callow workers eclosed about four months later. Workers apparently competed for reproduction. Aggressive interactions consisted of antennal boxing, pulling on legs and antennae, and biting. Aggression resulted in linear social hierarchies. During the observation period, repeated rank reversals occurred, hence it is unclear how stable hierarchies are. Furthermore, due to the low egg laying rates of individuals it is unknown how social rank relates to reproductive success. In one colony, five individuals were observed laying eggs over a period of eight weeks. The co-occurrence of fighting and thelytokous parthenogenesis is surprising but might be explained by the occasional occurrence of mated queens. Morphological queens have been observed in the field (S.P. Cover, pers. comm.) but their function is currently unknown.

CURLING, AGGRESSION, QUEENSHIP AND GENETIC RELATEDNESS IN THE NEOTROPICAL EPIPONINE WASP, *PARACHARTERGUS COLOBOPTERUS*

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Neotropical epiponine wasps establish large, multi-queen colonies by swarm founding. Queen numbers decrease over time such that very few queens are present to lay eggs when reproductives are produced (1, 2). High levels of aggression among queens have been implicated in this reduction of queen number (1). We combined videotapes of three colonies of *Parachartergus colobopterus* in the pre-emergence stage (when aggression is expected to be great) with DNA microsatellite-based estimates of genetic relatedness. Because we had 11 DNA microsatellite loci with 3 to 15 alleles each, we were able to obtain very precise estimates of relatedness among nestmates (3). As expected, queens were full sisters. Genetic relatedness among the workers averaged 0.2. We identified several aggressive behaviors. We also identified a submissive behavior, in which a wasp curls over on its side and exposes its abdomen, that occurs primarily when the wasp is being attacked. Certain females were much more aggressive than others, and directed their attacks nonrandomly. However aggression did not have a simple relationship to either genetic relatedness or reproductive status.

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**AGGRESSIVE INTERACTIONS AMONG GAMERGATES IN
QUEENLESS PONERINE ANT *AMBLYOPONE* SP.
(*RECLINATA* GROUP)**

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Social organization of colonies in the primitive ponerine ant *Amblyopone* sp. (*reclinata* group) was studied in Bogor, west Java, Indonesia. *Amblyopone* sp. has some unique characteristics of social organization among tribe Amblyoponini: morphological queens are lacked and some mated workers (gamergates) reproduced [1,2] and workers show an elegant recruitment behaviour for prey retrieval [3]. The colonies consisted of 97 workers on average and between 1 to 18 workers were inseminated and produced eggs. Degree of ovarian development of gamergates was not so different among gamergates within each colony, however, great variation was observed among colonies. This was correlated with number of virgin workers per gamergate. Among gamergates, aggressive antennation was frequently observed. The frequency of antennation greatly varied among colonies; the frequency was larger in the colonies having many gamergates than in that having a few gamergates. A linear order was constructed by the antennation among gamergates, although there were many reversal interactions. Higher-ranked gamergates had one to three developed oocytes while three low-ranked gamergates had no developed oocytes. Since such sterile mated workers were rarely found in the field, low-ranked gamergates may be expelled from their colonies.

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**REPRODUCTIVE DOMINANCE IN A PRIMITIVELY
SOCIAL ALLODAPINE BEE, *EXONEURA BICOLOR*.**

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In general, agonistic interactions are more commonly observed in social species where colonies are small, there are no morphological differences between females and sociality is facultative. *E. bicolor* possesses these characteristics yet aggression does not appear to be responsible for hierarchy stability. Reproductive hierarchies develop well before brood rearing commences in montane populations of *Exoneura bicolor* and overt aggression between females has been observed only rarely. Both adult eclosion order and pheromones have been implicated in the reproductive hierarchies which develop over autumn¹. One of the theories proposed to explain hierarchy stability is based on interpretation of wing wear exhibited by the inseminated, large ovaried female (principal egg layer) in overwintering nests. If the reproductively dominant female takes on the risky role of collecting food (extra-nidal activity causing wing wear) her chance of dying before producing eggs increases¹. A subordinate could then reproduce without facing extra-nidal risks herself. In this study newly eclosed bees were marked to identify both their eclosion order and the nest to which they belonged. No difference in the survival of females from autumn nests was found between bees of different eclosion orders. Data on foraging was collected from wild bees and from observations of experimental nests. It was found that the reproductively dominant female was unlikely to be the main food provider in autumn nests. Hence, there was a lack of support for the hypothesis which involves payoffs between subordinate and dominant females. The considerable nest swapping by bees housed in artificial nests and the survival through to winter of older generation females were both unexpected. The implications of these results and alternative explanations for the stability of *E. bicolor* reproductive hierarchies are discussed.

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MODE OF ACTION OF THE QUEEN PHEROMONE ON THE REPRODUCTIVE STATE OF WORKER HONEY BEES

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In highly evolved insect societies the reproductive division of labour between the fertile queen and the infertile worker castes is achieved through the subtle action of queen pheromones that inhibit ovary development and egg-laying in workers. The existence of pheromonal inhibition of worker reproduction is known for many ant, termite, bee and wasp species. But the pheromonal mode of action was completely unknown. Since juvenile hormone (JH) controls female reproduction in most insect species, we assumed that JH might act as a key regulating element in the transmission of the royal signal in the receiving worker. Components of the queen mandibular gland (QMG) in the honey bee, *Apis mellifera* L., known to be involved in the inhibitory function, were tested for the effect on the enhanced JH production of queenless workers (cf. Kaatz et al., 1992). The principal component of the QMG, 9-oxo-2(E)-decanoic acid (9-ODA), inhibits dose-dependently the biosynthesis of the gonadotropic JH in workers. 7.5 µg 9-ODA, representing about a twentieth of the queen's daily secretion, are equally effective as a live queen, natural QMG extracts and a blend of synthetic QMG components, and are ten times more active than the same amount of synthetic racemic 9-hydroxy-2(E)-decanoic acid. Other single components were not effective. The pheromonal impact of the queen on the worker's reproductive state is obviously mediated via the recipients endocrine system. Such a mode of action may also be present in other eusocial insects such as in bumble bees and in the termite *Zootermopsis flavicollis*. A relatively high amount of 9-ODA secretion is required for the inhibition. Older queens show reduced 9-ODA production and their reduced output may be associated with the superseding of the senescent queen by the workers. With regard to the problem of queen-worker conflict queen inhibitory pheromones have been frequently viewed as a means by which queens establish and maintain their reproductive dominance. But one cannot rule out the possibility that the honey bee queen pheromone serves as a means for workers to monitor her presence and reproductive performance in order to adjust their own reproductive activity in a way that maximizes their inclusive fitness (cf. Keller and Nonacs, 1993).

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INTRODUCTION : ECONOMICALLY IMPORTANT TERMITES IN URBAN AREAS WORLDWIDE

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In nature, termites are extremely beneficial insects as they convert cellulose to its elemental state. However, they are classified as pests when they damage man-made products and structures. Termites cause extensive monetary losses throughout the world. Edwards and Mill (1986) estimated that \$1.92 billion (U.S. dollars) was spent for termite pretreatments and remedial treatments worldwide, with the majority of these costs borne by people in the United States, India, and China. However, it is impossible to precisely determine the total economic impact of termites, which includes costs of prevention and control, as well as repair or replacement of termite damaged items. Of the ca. 2,200 termite species worldwide, only about 4% cause significant damage to buildings (Edwards and Mill, 1986), and their distribution varies among geographical regions (Harris, 1961). In the North Temperate Zone, subterranean termites in the genus *Reticulitermes* are the predominant economic pests. In North America, *R. hesperus* and *R. tibialis* occur in the western regions, whereas *R. flavipes* predominates in the Eastern U.S. and also in Ontario, Canada. *R. lucifugus* is widely dispersed in the Mediterranean regions, whereas *R. santonensis* and *R. flavipes* are important, but regional pests. *R. speratus* occurs in China and Japan. *Heterotermes* replaces *Reticulitermes* in warmer regions, including the Southwestern U.S., Central and South America, the Caribbean, and India. *Nasutitermes* are occasional pests found in most of Central America and the Caribbean. Drywood termites are serious pests south of 30° N latitude, and *Cryptotermes* are particularly widely dispersed. The most vigorous genus, *Coptotermes*, predominates in tropical America, the Far East, Japan, and Australia. *Macrotermes* and *Odontotermes* occur in Africa, India, and South-east Asia. It can be seen that primitive species, particularly the Rhinotermitidae, are economically important in urban areas worldwide. One of their most important biological characteristic appears to be their ability to produce neotenic reproductives. As termites have evolved (Termitidae), their ability to produce neotenics and to adapt to new environmental conditions has been restricted.

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ECONOMIC IMPORTANT TERMITES OF CHINA AND HONG KONG AND THEIR CONTROL

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Out of the five hundred plus species of termites recorded from China, approximately one-fifth can cause economic losses of various extent. The major species that cause serious damage to wooden structures and products are *Coptotermes*, *Reticulitermes* and *Cryptotermes*. In addition, *Glyptotermes*, *Incisitermes*, *Hodotermopsis*, *Ancistrotermes*, *Microcerotermes*, *Nasutitermes* and *Xiaitermes* can also cause damage to certain extent. Termites species attacking landscape plants are mainly *Coptotermes*, *Reticulitermes*, *Odontotermes*, *Macrotermes*, *Glyptotermes* and *Neotermes*. *Odontotermes* and *Macrotermes* are the two major species that cause damage to soil dammed reservoirs. In Hong Kong damage to wooden structures is almost exclusively caused by *Coptotermes* spp. In some rare incidents, *Reticulitermes* and *Macrotermes* are also found to be the destructors. One major difference in damages to buildings between Hong Kong and the Southern part of China is that the occurrence of air-invasion by *Coptotermes* spp. are far more prevalent in Hong Kong. In China, prophylactic measures against termites through soil treatment is a very common practice. However such treatment is rarely carried out in Hong Kong. In densely populated cities, people are very much concerned about the potential adverse impact of termiticides such as sodium arsenite and chlordane which have very long residual effects. Thus chlorpyrifos and certain synthetic pyrethroids such as deltamethrin supplied by Roussel-Uclaf (France) and cypermethrin supplied by Zeneca (UK) are gradually gaining popularity. Be it in China or Hong Kong, remedial measures to treat *Coptotermes*-infested wooden structures in buildings is by injecting pesticide powder into termite galleries or other active areas such as termite tracks, nests and flight holes. Commonly used insecticides in China are arsenous acid powder and dustable powder of mirex. Drilling and injection of aqueous forms of insecticides (e.g. chlorpyrifos, deltamethrin and cypermethrin) are sometimes adopted in termite control and are more often performed in Hong Kong than in China. However, this method is less effective than powder treatment.

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SUBTERRANEAN TERMITE DAMAGE TO STRUCTURAL WOOD- WORKS IN A SEMI-ARID TROPICAL URBAN SYSTEM

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Damage caused by the subterranean termites to structural-wood and other articles in different types of houses was investigated in a semi-arid tropical urban system at Warangal. Sixteen species of termites were recorded within the urban area, of which six viz. *Coptotermes ceylonicus* Holmgren (*Rhinotermitidae*), *Odontotermes bellahunisensis* Holmgren and Holmgren, *Odontotermes brunneus* (Hagen), *Odontotermes redemanni* (Wasmann), *Odontotermes wallonensis* (Wasmann), *Microtermes obesi* Holmgren (*Termitidae*) were found damaging different structural wood-works such as door-frames and panels, window-sashes, joists, rafters, ceiling eaves, wall-shelves, wooden and bamboo supports, wooden boxes, and other articles such as photo-frames, books and papers, and electrical switch boards. *C. ceylonicus* damaged the wood-works eating up the inside wood leaving out thin outer shell being perforated irregularly with channel-like holes plugged with wood dust and excreta. The characteristic damage of *Coptotermes* was recorded even in newly constructed buildings of the University. Damage of *C. ceylonicus* to some important archives including service books and registers were noticed even inside an iron almirah. The damage of *Odontotermes* to structural-wood was under patches of irregular earthen sheets. They constructed shelter tubes on the walls as a line of communication between the subterranean nest and the wood-works. The damage under the earthen sheet was irregular with the wood being eaten into various depths and filled with soil in case of severe damage, and nibbled when the damage was superficial. There was no discernible difference in the patterns of damage of different species of *Odontotermes* and that of *M. obesi*. Among all the termites, *C. ceylonicus* caused serious damage leading to maximum loss. The termite damage was controlled by chemical treatment of the site at the foundation level, and the timber at the time of construction, or by drilling holes and treating the old buildings with chemicals.

TERMITE PROBLEM IN SÃO PAULO CITY - BRAZIL

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São Paulo the biggest south american city, with about 15 millions inhabitants, has a great problem with termites. Two species are the most frequent: the subterranean termite Coptotermes havilandi (Rhinotermitidae-Coptotermitinae) an introduced species and the dry-wood-termite Cryptotermes brevis (Kalotermitidae) a cosmopolitan species. The damage by C. havilandi is normally the greatest and attains besides the different woods applied in the building also non cellulosic materials as leather, tissues and plastics as those of electric cables. An important attack on living trees is also reported. The damage by C. brevis more limited than C. havilandi was sometimes great mainly in old buildings and libraries. From December 1973 to December 1993 we inspected 240 edifications in São Paulo City from which 120 were submitted to a remedial treatment. C. havilandi was present in 113 (47%) and C. brevis in 36 (15%). Both species were present simultaneously in 91 edifications (38%). The costs of remedial treatments for those 240 edifications is estimated on US\$ 3,350,000.00 but the real damage caused by termites in São Paulo City is unknown. More recently, in 1993, we have found Heterotermes sp (Rhinotermitidae-Heterotermitinae) in 3 edifications. Until now we have not found this termite attacking edifications in São Paulo City. On the other hand, we have yet reported their attack in the interior of the State. There are several conditions favorising termite attack in the edifications of the city. These conditions are tightly related to a lack of preventive measures and a misuse of wood in the construction. In Brazil treated wood is used only for sleepers, spools and poles for fences and rural electrification. Until 1990 remedial treatments was made using Chlorinated insecticides: Lindane, Chlordane, Aldrin, Dieldrin and Heptachlor. Pentachlorophenol was also used , as fungicide, until 1984 in mixture with one of those insecticides. Since 1990 it is used Pyrethroids and Organophosphorus insecticides, the former in wood and the later in soil treatments. Phosphine is always used as fumigant against dry-wood-termites. The problem of termites is aggravated by a large and indiscriminated use of insecticides by people who not take care with their hazard to human health and to the environment. São Paulo City has 156 interprises working on the control of urban insects (data from The Sanitary Vigilance Service-1992). A great number of them propose itself to control termites but they have not termitologistes in their staff neither the advice of one of these specialists. A Municipal Termite Control Program for São Paulo City could minimise the problems instructing peoples and interprises about these insects and their control.

DETECTION OF SUBTERRANEAN TERMITE NESTS WITHOUT EXCAVATION

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In termite control, recognizing the position and dimensions of subterranean termite nests are always of great importance. In fact, once the position and dimensions of the nest have been determined, from the surface of the ground, and without excavation, we can precisely recognize the location of the main nest chamber, which is occupied by the queen, king and a majority of colony members. This will make our work on termite control very successful and nearly non polluting to the environment. In this report, we will present: 1. Some features of termite nests in dikes and dams, and in buildings and living trees of Vietnam. 2. Principles of detection methods such as electrical, sonic, radioactive, and some other ones. The electrical method can be used for detection of big and shallow underground nests. The radioactive method is effective for determining the position and dimensions of the nest. Sonic detection shows us whether or not the colony is surviving. 3. Combined methods of detection, using the best points of the above listed methods, against different types of termites. This last technique has been applied successfully to control termites in buildings, dikes and dams, and living trees in Vietnam.

FORMATION OF THE REPRODUCTIVES IN *RETICULITERMES SANTONENSIS* FEYTAUD (ISOPTERA, RHINOTERMITIDAE)

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Reticulitermes santonensis is one of the most important economic species in France. It is widely distributed in urban and peri-urban areas of Western France (Vieau, 1993). The reproductive cycle of this species, which has been confused with that of *R. lucifugus grassei* Clément (Buchli, 1958), remains poorly known. At the end of winter and during spring, colonies contain short (N7) and long (N8) wing-pad nymphs which were considered to be the two last nymphal stages by Buchli (1958). Statistical analyses performed on these nymph populations collected in peri-urban areas showed that N7 nymphs did not molt into N8 nymphs. Dimensions of N7 nymphs (head width, prothorax width, femur and tibia lengths) were greater than those of N8 nymphs. It was the same for genital organs and endocrine glands. Just before the dispersal flight season (mid April-May), JH III levels were higher in N7 (65 pg/ individual) than in N8 (7 pg/ individual). We observed that N7 transformed into brachypterous neotenics while N8 differentiated into alate imagos. The alate population increased with colony size. Small colonies of 3000-10000 individuals (n=20) contained about 15% N7+brachypterous neotenics and 0,7% N8+alates whereas more populous colonies of 15000-25000 individuals contained 13,5% N7+brachypterous neotenics and 4% N8+alates. However, in western France, only colonies of *R. santonensis* with brachypterous neotenics were collected, and colonies headed by primary sexuals were never found, contrary to the situation in southwestern France for *R. lucifugus grassei* (Feytaud, 1955). The mode of reproduction of *R. santonensis* and its territorial distribution are those of introduced termite species (Lenz and Barrett, 1982).

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RESEARCH ON THE SWARMING FROM THE LABORATORY BREEDING COLONY OF *COPTOTERMES FORMOSANUS SHIRAKI* IN CHINA

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The Genus *Coptotermes* in China contains up to about over 30 species. The biology of *Coptotermes formosanus Shiraki* has been studied in detail in many aspects. It takes eight years for colonies of *C. formosanus Shiraki* in the Guangzhou region to complete a generation cycle from the pairing of the primary reproductive to the first appearance of alates in the colony. A pair of alates was established by authors on May 18, 1974. The first alate's swarming occurred on May 3, 1982. Alates have swarmed eight times in 1982-1993.

The colony first released on five times release occurred between May 3 to June 2, 1982: the sum total of 869 alates were counted. The second release occurred from May to June, 1985: about several hundreds alates released. The third release occurred from April 21 to June 4, 1987: the sum total of 27813 alates were counted. A similar number of alates 28663 left from the colony in six time flight between May 22 to July 7, 1988. The cold cloudy weather with drizzling rain impels to delay swarming by 15-20 days. The fifth release were 20337 alates from May 2 to June, 1989. The sixth release occurred May to June, 1991: the sum total of 17586 alates were counted. The seventh release the sum total of 5835 alates from May 15 to June, 1992. The eighth release were 20193 alates from May 29 to June 28, 1993.

Sex ratio: females lesser than males. The ratio of females was 9.52-41.60%, mean 24.36% in 1982-1991. But 1992-1993 has happened swarming alates, all of the individuals was males and actuan virtually no females.

TREATMENT OF MASONRIES AGAINST TERMITES: METHOD AND CONTROLS

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In France, the requirements for the control of termite infestation in buildings consist in treatment of: the soil, the masonries and the wood. Although data on the effectiveness of soil insecticides have been published, no data exist concerning the effectiveness and durability of these insecticides in contact with masonry. A working group of the French Wood Preservation Association (AFPB) has developed a method for laboratory evaluation. This method and results obtained will be published. In practice, since the ban of aldrine, the chief problems encountered by the PCO in situ concern masonry treatment. In fact, many active ingredients found on the French market are not stable in basic and damp conditions. Within the framework of the French PCO Agreement (Approval CTB-A+), for the surveys undertaken with reference to this company's activities, it has been necessary to evolve a biological method for controlling the durability and the correct application of the insecticide to soils and walls. This method will be explained and the results of controls carried out during the last two years will be discussed.

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WOOD PRESERVATIVES AND INSECT PATHOGENS AS TOOLS FOR SUBTERRANEAN TERMITE CONTROL

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Subterranean termite (Isoptera: Rhinotermitidae) colonies are characterized by: (i) a cryptic nest structure at an unknown location in the soil, (ii) an extensive network of foraging galleries with many points of entry into nearby buildings, and (iii) a foraging population extending into millions of individuals. Soil insecticide applications provide a temporary barrier to foraging termites, but are difficult to apply and must be renewed at frequent intervals. Physical barriers (gravel or steel mesh) offer more permanent protection, but require careful installation and are of limited utility in remedial control. Combined use of unpalatable construction materials and baiting strategies to reduce local termite populations offers promise as an environmentally sound approach. Research with wood preservatives such as sodium borate and copper naphthenate against *Coptotermes formosanus* Shiraki indicates that preservative-treated wood should be considered "termite resistant" rather than "termite proof," and as only one component in a termite management strategy. Since subterranean termites live in a confined and humid environment, pathogenic fungi may be ideal bait control agents. Although destruxins isolated from the fungus *Metarhizium anisopliae* proved too repellent for use in baits, screening of six living isolates of *M. anisopliae* and *Beauveria bassiana* identified several isolates of each with no apparent repellency and the slow mortality pattern desirable in termite baits. Termites can vector as many as eight million conidia per worker, greatly exceeding LC_{95} values of 490 to 20,000 conidia per termite, and transmission to other colony members has been demonstrated.

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ALTERNATIVE PROTECTION OF JAPANESE HOUSES FROM SUBTERRANEAN TERMITE INVASION

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Economic losses caused by attacks of two subterranean termite species, *Coptotermes formosanus* Shiraki and *Reticulitermes speratus* Kolbe, are estimated more than one billion US dollars per year in Japan. Typical Japanese houses are timber-frame constructions on the concrete base (wall footing, 30-50 cm above the ground level) so that crawl space is present between floor and ground. To prevent termite invasion through crawl space, soil poisoning and timber treatments with chemical formulations have been widely employed. Because of the treating difficulties in the crawl space, the risk for operators and residents and environmental hazard, various alternative treating methods have been recently developed in Japan.

(1) Foaming treatment:

Termiticidal chemicals and organic solvent are formulated with foaming agents. The formulation is converted into foams by a special apparatus, and the foams spread out evenly throughout the crawl space. Pest control operators can treat both soil and building timber from the outside of an existing building. This method is supposed to reduce the risk for the health of operators and residents, and to shorten the treating time.

(2) Anti-termite sheet:

Termiticides are mixed with synthetic polymers, and are formed into sheets with a thickness of approximately 0.2 mm. The sheets are layed over soil surface in the crawl space. The sheet is expected to repel termite invasion and to keep the crawl space dry. As a matter of course, there is no possibility to contaminate the air in this method. The two-layer sheet consisting of humidity-protecting layer (upper layer, polyethylene sheet with a thickness of 0.1 mm) and termiticide-containing layer (lower layer) has been commercialized as well. In this case, chemicals are slowly released into soils from the underside of the layer by water condensation.

(3) Anti-termite resin layer:

Instead of anti-termite sheet described above, termiticide-containing resin layer on soil surface is applicable to prevent termite tunnelling. Synthetic resin emulsion containing termiticides is mixed with hardening agents, and is sprayed over soil surface of the crawl space. The emulsion is hardened within a couple of hours, and confirms a highly persistent resin layer with termiticides. Because chemicals fix in resin, the air pollution after treatment is negligible. The layer also prevent moisture uptake from soil.

(4) Forced ventilation in the crawl space:

As subterranean termites need high humidity for their feeding activities, ventilation of the crawl space is a very important factor to depress termite invasion. Recently forced ventilation system in the crawl space has been developed. This system consists of a few small automatically-controlled electric fans which are attached to concrete base. Other alternative treating methods would be more effective when they are applied in combination with this ventilation system.

**CURRENT PRACTICES AND DEVELOPMENTS IN AUSTRALIA
FOR THE PREVENTION AND CONTROL OF TERMITE
PROBLEMS IN BUILDINGS**

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A notable range of methods for the protection of buildings from subterranean termites is currently either in use or at different stages of development in Australia. (A) Preventive measures, incorporated at the design and construction stage of a building include: (1) Physical barriers: stainless steel mesh, graded granite; other systems under development; (2) Chemical soil barriers (2a) Chemicals applied to soil directly: cyclodienes for restricted times or locations only; chlorpyrifos unrestricted in buildings with raised subfloors, other chemicals, notably synthetic pyrethroids, and novel compounds such as imidacloprid under assessment or registration pending; (2b) Chemicals applied via a reticulation system for slab-on-ground constructions, two systems: porous pipes or evenly spaced injectors; chlorpyrifos (2c) Matrices other than soil as carriers for chemicals: fibrous "blanket" and plastic materials, under development; (3) Termite resistant materials (inclusive preservative-treated wood); (4) Building design such as exposure of slab edge, removable skirting boards etc. - (B) Treatment of infestations in existing buildings: (1) Restoration or establishment of chemical soil barriers: direct application, slab-drilling; reticulation systems; chlorpyrifos, other compounds under development; (2) Location and direct treatment of colonies; (3) Dusting: arsenic trioxide, alternative products under development; more recently in conjunction with trap-and treat systems to aggregate termites first; (4) Bait-systems (matrix and slow-acting toxicant): one system with limited application; under development; (5) Biological control: the fungus *Metarhizium anisopliae* and the nematode *Hterorhabditis* sp., under development. Much research on termite control in Australia focusses on non-chemical preventive measures, on methods permitting safer application of chemical barriers, and on control of infestations in existing buildings through trap-and-treat and bait-systems.

LOW COST TERMITE CONTROL IN BUILDINGS FOR THE RURAL AND URBAN POOR IN AFRICA

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In Africa there is widespread attack on buildings by termite species such as *Macrotermes*, *Microtermes*, *Odontotermes* and *Coptotermes*. *Psammotermes*, *Anacanthotermes* and *Microcerotermes* are the major pests in the semi-arid regions while the drywood termite *Cryptotermes* can be a serious pest in humid coastal or lakeside areas. These termites cause considerable damage to houses, stores, factories, business and agricultural premises. Until recently building damaging termites were controlled by the organochlorine insecticides but concern over their effects on the environment has led to them being withdrawn or banned from use in many countries. The organochlorine insecticides were very cheap and easy to apply but replacement insecticides, such as chlorpyrifos, permethrin and cypermethrin, are considerably more expensive and consequently their use is restricted almost entirely to high value urban buildings although, even here, many builders still depend on remaining stocks of aldrin and dieldrin. In low cost urban and rural buildings the owner has to balance the cost of labour, materials and chemicals for termite treatment against the social and economic value of the building. Because of this, such buildings are frequently built without any form of termite protection and are either repaired or rebuilt when damage takes place. In some cases entire villages are relocated when termite damage becomes too great. However, there are various low cost alternatives to chemical treatment and these are not used as widely as they should be. Some were used extensively up till about fifty years ago but fell into disuse following the introduction of the organochlorine insecticides; some have been developed recently and their use has not spread to some of the areas where they are most needed; while others were developed by the indigenous population and are only used locally. Among the methods discussed in this paper are the use of physical barriers (such as termite shields), resistant or treated timber and construction techniques.

ENVIRONMENTALLY-FRIENDLY, GROOMABLE COATINGS FOR CONTROL OF TERMITES AND OTHER SOCIAL INSECTS

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A topically-applied, groomable, resin-based coating containing the slow acting toxicant, sulfluramid, was developed and tested for the control of the eastern subterranean termite, *Reticulitermes flavipes*. Field trials at 20 sites in Metro Toronto during the summer of 1993 resulted in 100-60% suppression of average weekly trap yields at all sites after one, two, or three applications. Lab tests were also conducted with the carpenter ant, *Camponotus pennsylvanicus*. Ninety percent mortality was recorded after 10 weeks at a ratio of 1 treated ant per 100 untreated (4 replicates) compared to 8.5% mortality in the controls. Groomable coatings have distinct advantages when compared to sprays, soil insecticide applications, and baits. Direct application to the insect is the ultimate in "targeting the pest". Because the insects are treated directly there is an enormous reduction in the quantity of pesticide required and in the environmental contamination which is usually associated with soil termiticides, sprays, and broadcast applications of bait pellets. There can be a thousand fold increase in the amount of toxicant applied to individuals compared to the amount which would be ingested by bait feeding. The number of individuals directly treated is only limited by the number that can be trapped. The mobility of the treated insects results in a greater dispersal and distribution of toxicant compared to stationary baits. Because of the sudden and massive input of toxicant, and its rapid transmission into the social insect population it is more difficult for the insects to wall off or isolate affected areas than would be the case with the slower and more localized infusion of toxicant via baits. The existence of groomable coatings will increase the need for control protocols based on a more detailed knowledge of the social biology of pest insects by pest control operators. To exploit this technology there will be an increasing demand for knowledge about how to locate nests and foragers, how to trap nesting and foraging social insects, how to maintain trapped populations, and how best to treat and release them. There will also be a greater need to understand grooming and grooming stimulants. Grooming is an important exploitable behaviour or "fatal flaw" in social insects. Groomable coatings will be utilized within specific trap-treat-release protocols developed for each major social pest. Generalizing, it would appear that social insect colonies can be strongly suppressed or eradicated by this method if 1-5% of the population can be trapped.

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OVERCOMING THE REPELLENCY OF BAIT TOXICANTS IN TERMITE CONTROL

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The bait-toxicant technique for the local control of subterranean termites in urban areas has been regarded for more than 25 years as a less hazardous alternative to the traditional application of biocides to the surrounding soil or to the wooden structures of buildings. However, due to the repellent or antifeedant properties of the sparse active ingredients with the desired slow action the bait-toxicant technique is still not ready for broad application. By microencapsulating the active ingredient we succeeded to suppress the typical avoiding reaction which termites show very soon when the baits are treated with standard insecticides like permethrin. In tests which were performed with laboratory colonies of the subterranean termite species *Reticulitermes flavipes* and *Heterotermes indicola* corrugated cardboard served as baiting material. After treatment with microencapsulated permethrin the baits did not show signs of loss in attractivity. The gradual release of the active ingredient from the microcapsules and thus the delayed toxic effect permitted by trophallaxis and grooming an efficient distribution of the microcapsules throughout the termite colonies and eventually extinguished the colonies. In 1992 a practical control measure was started at an urban site in Germany heavily infested with *H. indicola* which had been introduced from the Far East some 40 years ago. Using the baiting technique with microencapsulated permethrin the numerous termite groups at that location could be drastically reduced. Thus, with the microencapsulation technique some of the well known active ingredients not necessarily belonging to the slow-acting type may be used as bait toxicants for the control of termites. By modifying the walls of the microcapsules and the amount of biocide the technique can be adjusted to the specific needs of different termite species.

FATE OF SUBTERRANEAN TERMITE POPULATION AFTER BAITING WITH SLOW-ACTING TOXICANTS: MANAGING SUBTERRANEAN TERMITE POPULATION IN URBAN ENVIRONMENT

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Field applications of termite baits with various delivery systems and active ingredients have been tried against colonies of the Formosan subterranean termite, *Coptotermes formosanus*, and the eastern subterranean termite, *Reticulitermes flavipes* in urban southeastern Florida. Responses to these applications varied from colony to colony. Populations and foraging activity of several colonies of *C. formosanus* were reduced by bait applications but bounced back later when baiting stopped. Population of one *R. flavipes* colony was reduced from 2.8 million to 26,000 foragers by a baiting application, and continued to decline in the following years. Practical considerations of population reduction techniques such as baiting in populated urban environment will be discussed.

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CONTROLLING TERMITES WITH THE CHITIN SYNTHESIS INHIBITOR, HEXAFLUMURON: A SUMMARY OF FIELD RESEARCH

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Research was initiated in 1993 at a number of sites across the United States which was designed to confirm the activity of the slow-acting IGR, hexaflumuron, against several species of subterranean termites (Isoptera: Rhinotermitidae). At each site, individual termite colonies were identified and characterized. After the termite colonies foraging population, foraging territory, and feeding activity was established, the toxicant containing matrix was introduced and the termites were allowed to consume it until no more activity was observed. In all cases the termite colony was either eliminated or drastically reduced. Monitoring of these colonies continues in 1994.

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COMMUNICATIONS ORALES

CONTRIBUTED PAPERS

ECOLOGICAL SIGNIFICANCE OF RECRUITMENT BEHAVIOUR
IN THE GENUS CAMPONOTUS (HYMENOPTERA:FORMICIDAE)

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Recruitment behaviour is described in many ant societies. It enables individual workers to get their nestmates to move to an intended destination, e.g. a new nest site, a territorial intruder or new food sources. Patterns of recruitment communication in seven species of the genus *Camponotus* were analysed and compared. The ecological conditions connected to foraging and emigration to new nests were recorded. Observation of spontaneous and induced recruitment acts and additional laboratory studies showed that chemical and mechanical signals are utilized in the communication process. Similar ecotypes use the same recruitment strategies. Highly specialized species like *Camponotus texens*, weaver ants that live strictly arboricolous in silk pavilions and feed almost exclusively on the exudations of their trophobiotic partners, never show recruitment activity connected with foraging or emigration behaviour, although they use an effective mass recruitment system to drive away intruders. Generalistic species, like *Camponotus auriventris*, that build simply constructed soil nests and exploit a variety of different food sources, have a functional orientated group recruitment system. Sympatric *Camponotus* species from Westmalaysia (*C. texens*, *C. gombaki*, *C. auriventris*, *C. gigas*) are compared with palaearctic species (*C. vagus*, *C. herculeanus*, *C. cruentatus*).

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**SPERM UTILIZATION IN THE DESERT LEAF-CUTTER
ANT *ACROMYRMEX VERSICOLOR***

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In the desert leaf-cutter ant *Acromyrmex versicolor* mating takes place in precisely timed, dense aerial swarms. Before the flight, the seminal vesicles of each male contain between 30 and 50 million sperm, whereas the final amount of sperm stored in the female spermatheca is only around three million. Nevertheless, sperm counts performed at different times during the mating flight clearly showed multiple mating for both males and females. Queens mated three to four times and rejected further males under experimental conditions. Up to 40 million sperm were found in the female reproductive tract shortly after the last mating. All but the three million sperm stored in the spermatheca disappear from the reproductive tract during the first days of colony founding. To find out which of the sperm transferred to the female in successive matings finally make their way to the spermatheca, females mated to three or four males were allowed to found colonies in the laboratory. Random amplified polymorphic DNA analysis of all presumptive fathers, the queen, and their offspring showed that all the males successfully contributed sperm to the production of the first generation of workers. There was no evidence for sperm precedence.

CAN OPTIMAL FORAGING THEORY BE USED AS A TOOL FOR BUMBLEBEE FLIGHT ENERGETICS ?

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Optimal foraging theory has been successfully applied to the foraging behaviour of a variety of animals. In honeybees (*Apis mellifera*), which rarely fill their honey crop during foraging, it was used to analyse nectar foraging in an artificial patch. Nectar gathering behaviour could be best predicted by assuming that the foraging bee optimises the ratio of net energetic gain to foraging costs ($(B-C)/C$; B = benefits, C = costs; Wolf and Schmid-Hempel, 1990). Bumblebee workers (*Bombus terrestris*) also rarely fill their crop when foraging in natural environments. In field observations, I found that nectar foragers ($n=57$) with a mean unloaded body mass of 210 ± 39 mg (range: 118-283 mg) returned to the colony with an additional 33% of their body mass in nectar. To analyse the energetics of bumblebee foraging, 13 individuals were trained to fly to an artificial patch where the quality and quantity of the sugar water offered could be controlled. The bees returned to the colony having visited many fewer flowers than the maximum possible. The mean number of flowers required for the bees to fully load up was 122, but only 10.2 flowers were visited on average. This is even fewer than predicted by models of optimal foraging theory in which I assumed that bumblebees use the same 'currency' as honeybees ($(B-C)/C$). In these models, the costs of foraging have been simulated by using energetic data obtained from bumblebee flights in laboratory experiments (Cooper, 1994). Bumblebee foraging behaviour can be accurately predicted by optimal foraging modelling only if the actual metabolic rates of foraging bees are only 30 to 50% of the values measured using respirometry. These predictions will be tested in the future using the doubly labelled water method.

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SEMIOCHEMICALS OF *VESPA MANDARINIA* (HYMENOPTERA: VESPIDAE)

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The giant hornet, *Vespa mandarinia* is the largest vespine species in the world. It has interesting mating and foraging strategies. This paper discusses several semiochemicals found in *V. mandarinia* and their adaptive significance.

1. Mating strategy: Two step—pheromonal regulation of mating behavior is species—specific feature of this hornet. Workers encourage the mating success of virgin queens by producing a male—aggregation pheromone to maximize inclusive fitness. The nest is constructed underground and many males are attracted to the entrance where they attempt to copulate with the departing queen. The queen produces a caste—specific sex pheromone which evokes mating by males. These pheromones were collected using absorbent (Tenax TA) and were analyzed by GC—MS. More than 30 chemicals were identified, but the active principles have not been determined yet.

2. Foraging strategy: Only this *Vespa* species has evolved mass—attack foraging on social bees and wasps as a source of protein. The first forager secretes a foraging—site marking pheromone from its van der Vecht gland around the site before the mass attack starts. Sympatric prey “read” the pheromone and show an adaptive response. *Apis cerana japonica* perform chemical and acoustic mass defense. *Polistes rothneyi* absconds and rebuilds several small nests around the original nest. *V. mandarinia* can also locate volatile chemicals emanating from fermented syrup. Head—space gas analysis identified more than 40 chemicals and five active substances were determined by EAG assay. Kairomone from the hornet can be used to control it.

RED WOOD ANTS AND FOREST PHYLLOPHAGOUS INTERACTION

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In result of research on protection of forest insects we came to conclusion that needles and leaf-eating insects and their entomophages are reserved at the same stations. It puts a very serious problem of predator-prey interaction (Abrams, 1992). It is important to find a mechanism as a result of which predator can keep the quantity of prey population on the same level or even increase it. Ants do not destroy completely all populations of phyllophagous. We do not know exactly what part of population of phyllophagous is not touch by ants. This problem was studied from one point different quality of ants, nobody studied different quality of phyllophagous. We studied interaction of red wood ants *Formica polyctena* and *F. pratensis* with pine moth (*Dendrolimus pini*) in pine stands of Voronez district. We found out that predatory of ants is different with active or inactive part of population of pine moth. Ants are hunting in the day time, choosing only moving larvae. The active part of population of pine moth at day-time is immovable. It moves only at dusk (Malyshev, 1991). *F. pratensis* moving by stem and upper part of branches do not notice larvae sitting immovable on the bottom of branches. *F. polyctena* attacks old instar larvae in a manner of well-organized battle: one part attack moving larvae in needles, when the other is waiting for those who fall down on the ground. Thus red wood ants eliminate inactive part of population of pine moth leaving safe the active one.

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MYRMECOCHOROUS DISPERSAL DISTANCES: A WORLD SURVEY

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It has been suggested the possibility that safe-sites distribution and myrmecochorous dispersal curves from the Northern Hemisphere are markedly different from those of Australia + South Africa. A survey has been made on all available data on ant dispersal distances of seeds of myrmecochorous species: individual data, means, published maps and unpublished own data have been treated together; several patterns emerge though its actual relevance from the plant's point of view is not immediately apparent. When considering weighted data, the mean dispersal distance is 1.13 m (n=1402); data from published maps, dispersal curves and own data yield a mean of 1.16 m (n=593); the median is of 0.83 m. Weighted data for the Northern (N) Hemisphere have a mean of 0.98 m (n=836) vs. a mean of 1.33 m (n=566) for the Southern (S) Hemisphere. The mean based on maps and dispersal curves are 0.82 m (n=447) for N and 2.15 m (n=146) for S; medians are 0.57 m for N vs. 1.62 m for S. Comparison of distances from sclerophyllous (Sc) vegetation vs. mesophyllous (M) vegetation reveal also a difference: weighted data for Sc is 1.22 m (n=753) vs. 1.06 m (n=603) for M. Means based on maps and dispersal curves are 1.44 m (n=333) for Sc and 0.78 (n=260) for M; medians are 0.89 for Sc and 0.59 for M. A taxonomical pattern has also been detected; distinct subfamilies of ants disperse at various distances: Formicinae 2.26 m (n=70), Myrmicinae 0.76 m (n=752), Ponerinae 1.63 m (n=335) and Dolichoderinae 0.76 m (n=114). Main conclusions are 1) ant dispersal distances are short range and the bulk of data probably represent seed dispersal to nearest nest; 2) a small fraction (4%) of seed can be transported > 11 m; this probably represents seed transported to 2nd, 3rd,... nearest nest. A taxonomic effect seems to exist but since ant communities are usually diverse and comprise usually a minimum of two subfamilies (Formicinae + Myrmicinae) this effect is probably of no relevance to the plant. Though admittedly a fraction of a total, the number of safe-sites represented by nests of dispersing ants, seems to be more abundant in the Northern Hemisphere, more abundant in Mesophyllous forests. It remains dubious if quantitative, numerical differences when considering a geographical factor or an ecological factor are indeed important for the plants.

DRUPADIA RAVINDRA AND *D. THEDA* (LEPIDOPTERA: LYCAENIDAE): CONTRASTING SYSTEMS OF MYRMECOPHILY AMONG TWO CLOSELY RELATED BUTTERFLY SPECIES

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The life-cycles of the south-east Asian lycaenid butterfly species *Drupadia ravindra* and *D. theda* were studied in a rain forest near Kuala Lumpur (West-Malaysia). The two closely related species coexist in the same habitat. Field observations, laboratory experiments, and field experiments were carried out to investigate oviposition behaviour, host plant ranges, and relationships with ants. Both species utilize a wide range of food plant species covering eight plant families. There is a remarkable overlap in host plant ranges, as well as in plant parts used for oviposition and larval nourishment. Regarding myrmecophily, however, these two species show strikingly different adaptations. Field observations and experiments with *D. theda* clearly demonstrate an obligatory and specific relationship with two *Crematogaster* species. Female *D. theda* butterflies detect the presence or absence of their specific ant partners on hostplants and use them as oviposition cues. At appropriate locations, larger egg-clusters (up to five eggs) are laid. Communication signals of *D. theda* caterpillars are effective only towards workers of these two *Crematogaster* species; even other species of the same genus ignore the larvae. *D. ravindra*, in contrast, is facultatively myrmecophilous. Up to now ants from nine genera in three subfamilies have been found tending *D. ravindra* larvae in the field and one additional ant genus formed stable associations with the caterpillars in the laboratory. *D. ravindra* females do not use ants as oviposition cues: the suitable part of a hostplant is sufficient to induce solitary egg-laying. Our observations indicate that both *Drupadia* species have similar demands concerning habitat and hostplant use, but with regard to myrmecophily they show remarkable differences in oviposition behaviour and communication abilities of larvae towards ants. Therefore resource partitioning among these two butterfly species is mainly mediated by their contrasting patterns of mutualism with ants.

THE ORGANISATION OF A DIVERSE COMMUNITY OF AUSTRALIAN ANTS

A. J. Pontin

Coexisting species of ants may form a mosaic of non-overlapping territories as described by Way (1953) and Leston (1973) or they may have interspersed nests with overlapping foraging territories because intraspecific spacing leaves room for nests of other species as in the case of *Lasius flavus* and *L. niger* (Pontin 1961). Some behaviour or chemical means of avoiding interspecific interference is similarly necessary when foraging. A more complex community of 20+ species in a seasonally dry secondary woodland in New South Wales was mapped in spring 1991 and again in 1993 for nearest-neighbour analysis to test which theoretical possibility was most realistic. Only a few of the larger epigaeic species were numerous enough and amenable to analysis, but the interspersal hypothesis fitted their behaviour and distribution well.

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TERMITES FROM NORTHEASTERN BRAZILIAN FORMATIONS

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The Neotropical Region has been considered one of the richest in termite species, although it is very poorly known, specially for some areas as the semi-arid Brazilian Northeastern. In the literature there are only 8 genera and 11 species listed for this region. I conducted two collecting trips to the area to fill gaps in the MZUSP Collection and to compile field observations, mainly about nests. I also intend to compare different areas, in terms of diversity and richness of termites when all the samples are determined till species level. I visited 8 localities for one week each, covered by open formations (*cerrados and caatingas*), a dry forest with lianas, an altitudinal field, and a special kind of high forest. For qualitative collecting I looked for termites in every conceivable microhabitat. To record information on nests I took pictures and registered site, dimensions, color, hardness and the presence of: royal chamber, nymphs, alates, termitophiles and/or other animals. For the quantitative collecting I marked a transect, and along it 6 rectangles of 2.5mX4.0m spaced by 10m from each other on alternate sides of the transect, totalizing 60m² for each locality. All microhabitat in each plot were investigated leaving the area virtually clean. Of the 1000 samples collected, 75% I have identified till species level. There are 138 species (83 new) and 52 genera (12 new) of Termitidae, Rhinotermitidae, Kalotermitidae and Serritermitidae. I have copious information on nests along with other field notes for most samples. Considering the 518 described termite species in the Neotropics, the numbers showed above indicate that this may be actually the richest region in the world.

ANTS AS ECOLOGICAL INDICATORS: THE CASE OF SEMI-ARID NORTHEASTERN BRASIL

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The semi-arid Brazilian Northeast is one of the poorest known ecosystems in the Neotropics - a region which is known as one of the richest in ants in the world. Most species are known only from a few localities, but it is not known if the fauna is really composed of species with restricted distributions or this is an effect of our meager knowledge on distributions. To address this question I visited 11 localities for one week each, covering the most important environments in the region: 4 *cerrados* (savanna), 2 *matas-de-cipó* (dry forest with lianas), 2 *campos rupestres* (tropical altitudinal field), and 3 *caatingas* (seasonally impoverished dry forest). In each locality the ant fauna was surveyed qualitatively and quantitatively. Along a transect of 250m I set pitfall traps at 25 evenly spaced points. Two meters at the right and 2m at the left of each point I offered sardine baits on the ground and honey-water on a branch at 1.5m high baits, for 2 hours. At the other side of the transect the baits were offered in opposite order. This procedure was repeated at night. Five samples of litter ($1m^2$) were collected in each locality for Berlese funnel treatment, summing then 230 samples for each locality. After this I collected in every conceivable microhabitat, sweeping litter, breaking twigs, opening rotten logs, and so forth. A total of 370 morph-species was collected (identified till species level when possible), including several undescribed forms. Summing up all data gathered for each morph-species, including bait quality, habitat and time of the day, resulted in valuable information on species preferences and habits. Analyzing the results with Morisita similarity indexes and comparing these indexes with the distance among localities revealed that similar vegetation types support similar faunas, even from distant areas. Closer areas with different vegetation types may house very different ant faunas.

SHIFTS IN WORKER TASK PERFORMANCE REFLECT CHANGED REPRODUCTIVE POTENTIAL IN HONEY BEE, *APIS MELLIFERA*, COLONIES

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Variability in the division of labor among workers in social insect colonies is affected partly by colony conditions. Recent loss of the queen in a honey bee (*Apis mellifera*) colony is a condition which affects its reproductive potential over both the short term, approximately three weeks, and the long term following the first three weeks. Changes in short-term relative to long-term reproductive potential that follow queen loss may be expected to influence shifts in worker task performance. Indeed, worker honey bees forage for pollen less, cannibalize brood, and are more defensive shortly after their queen has been lost. A honey bee colony rearing queens in preparation for swarming also has a change in its short-term relative to long term reproductive potential. As with a recently queenless colony, this change would be expected to influence shifts in worker task performance. In fact, *A. mellifera scutellata* colonies in Botswana are more defensive when rearing queens prior to swarming. Both cases reflect increased investment in short-term relative to long-term reproductive potential. Such effects may be evident in other monogynous social insect colonies.

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DIVISION OF LABOR, ENZYME ACTIVITY, JUVENILE HORMONE TITER AND THE PLASTICITY OF TASK SHIFTS IN HONEYBEE SOCIETY.

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In European honeybee, *Apis mellifera* L.(A.m.) society, division of labor (age polyethism) is a characteristic phenomena, which was regulated by Juvenile hormone (JH) increase in haemolymph with age.

Haemolymphal JH titer determined by a micro-HPLC system. Following equipments and conditions were used for the micro-HPLC: Micropak column (1.5 mm i.d \times 250 mm in length) packed with μ s-Finepak SIL CN (JASCO); a JASCO 880-PO HPLC pump with an ML-425 micro-injection system (1 μ l sampling loop); a JASCO 875-UV detector (1 μ l flow cell) at 217nm; a JASCO 802-SC system controller and a HITACHI 056 recorder at 1mV full scale; an *n*-hexane-*n*-butanol mixture (100 : 0.58) was used as the developing solvent at 0.1ml/min flow rate and 55 kg/cm² pressure.

JH-III titer is influenced by age and season; it increased with age in all seasons and the titer in summer bee were higher than the corresponding bees in winter and in rainy seasons, during the time the titer remained at low level. Positive correlation was demonstrated among JH titer, age and kinds of labor in summer and winter bee. In Japanese honeybee (*Apis cerana japonica* Rad.), JH titer were determined by the micro-HPLC method.

When A.m. day-0 workers were treated by methoprene (JHA), guards and foragers appeared much earlier than control. Physiological changes (*in vivo* and *in vitro*) were also observed such as α -glucosidase (III) activity for honey production in the hypopharyngeal glands, which functioned to produce bee-milk when bees were young. These results indicate that physiological phenomena relating to tasks were governed directly by JH-titer, which increased with age. We examined whether production of the major source of bee-milk protein for in hypopharyngeal glands was controlled by the juvenile hormone or not.

DO MONOMORPHIC ANTS EXHIBIT SIZE POLYETHISM?

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Division of labor (or polyethism) among workers in social insect colonies can be influenced by various factors including age, size, and genetic differences. Age polyethism is widespread, and as workers age they typically progress from performing tasks within the nest (e.g. brood care) to riskier outside tasks (e.g. foraging). Size polyethism occurs more rarely and involves the differential performance of tasks by workers of different sizes, workers that are often distinctly polymorphic with a broad multimodal size-frequency distribution and strong allometric growth of various body parts (e.g. the head versus the alitrunk). However, size polyethism has also been reported in some monomorphic species, species in which workers exhibit a unimodal distribution of worker sizes that tends to be relatively narrow and associated with little or no allometry. I tested for age and size polyethism in the monomorphic ant *Leptothorax* (*Myrafant*) *longispinosus* Roger by measuring the head and alitrunk widths of workers that were either foraging or not foraging in 15 field-collected colonies, and by comparing the behavior of older, overwintered workers which were present in colonies when they were collected, to younger workers which eclosed in the laboratory. Foragers and nonforagers often differed significantly in size, but size and behavior were not consistently correlated across colonies: foragers were significantly larger than nonforagers in six colonies, significantly smaller in six colonies, and not significantly different in three colonies. Moreover, age cohorts also differed significantly in size, and there was a significant association between age and behavior. These results indicate that this species exhibits age polyethism but not size polyethism. Worker size in this species appears to be a very labile trait that may be highly responsive to environmental variability, probably larval nutrition, such that colonies often consist of multiple age-cohorts with different size distributions. Age polyethism is nearly ubiquitous among social insects, and age-dependent size variability combined with age polyethism is likely to produce spurious correlations between size and behavior within colonies. Previous reports of size polyethism in monomorphic ants fail to consider this possibility and, at present, there is no conclusive evidence for size polyethism in any monomorphic social insect species.

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EFFECTS OF FOOD QUALITY AND HIVE TEMPERATURE ON THE THERMAL BEHAVIOR OF DANCING HONEYBEES

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The thermal behavior of round and wagtail dancing honeybees (*Apis mellifera carnica*) gathering sucrose solutions of 0.5 to 2 M concentration 30-506 m away from the hive was investigated under field conditions by the use of contactless infrared thermography (see References). During the stay inside the hive thoracic surface temperature (T_{th}) was in the range of 31.4 to 43.9 °C. Sucrose concentration of the food was influencing dancing temperature (T_d) in a nonlinear way. Foragers gathering 0.5 M solution showed an average T_d of 37.9 °C (SD=1.33, n=234 dances), whereas with 1 M solution T_d amounted to 40.1 °C (SD=1.11, n=402). With 1.5 M and 2 M solution average T_d s were 40.6 (SD=0.71, n=167) and 40.7 °C (SD=0.77, n=132), respectively ($P<0.0001$ compared to 0.5 M, U test). The variability of T_{th} was highest with 0.5 M and significantly lower with 1-2 M concentrations. T_{th} during trophallactic contact to hive bees was similar to dancing temperature at 1.5 M concentration but lower at 0.5 M, 1 M and 2 M concentration. During periods of distribution of food to hive bees the dancers' thorax cooled down by more than 0.5 °C much more frequently with 0.5 M solution (65 % of cases) than with 1.5 M solution (26 %). By way of contrast, heating the thorax by more than 0.5 °C was rather seldom with 0.5 M solution (2 %) but occurred with a maximum rate of 26 % with 1.5 M solution ($P<0.01$, Chi-square). Bees gathering 1 M or 2 M solution showed intermediate behavior. Dancers gathering higher sucrose concentrations compensated better for variations of hive air temperature. With 0.5 M solution T_d increased by 0.34 °C/°C increase of hive temperature. The increase was 0.22 °C/°C with 1 M solution, but only 0.12 °C/°C and 0.13 °C/°C with 1.5 M and 2 M solution, respectively. The results furnish evidence that dancing honeybees follow a strategy of "selective heterothermy" by tuning the level of thermoregulation to the needs of the behavior performed at the moment, increasing thoracic temperature if fast exploitation of high-quality food sources is recommended and lowering it if the ratio of gain to costs of foraging becomes more unfavorable.

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QUEEN REARING SUPPRESSION IN THE HONEY BEE - SECONDARY SIGNALS FROM YOUNG BROOD

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The presence of a single queen will suppress the rearing of new queens by a colony of honey bees, Apis mellifera L. Queen mandibular gland pheromone (QMP) is primarily responsible for this inhibition, and has been demonstrated using synthetic QMP which inhibited queen cell production for four days following queen removal (Winston et al. 1990). However, beyond day four, QMP suppression declines and queen cells are reared, indicating other signals are also important in relaying to the colony the queen's status. In 1993 we investigated the role of eggs and young brood as possible secondary signals to QMP. Thirty queenless colonies were each given one queen equivalent of QMP daily for ten days. Additionally, fifteen of these colonies received a frame containing young brood on days 2, 4, 6, & 8. Queenless colonies receiving only QMP were partially suppressed from rearing queen cells for four days and then began to rear on average 4.5 cells per colony over the next six days. The colonies receiving both QMP and young brood reared on average only 2.5 queen cells per colony over a ten day period. The number of queen cells reared by colonies receiving QMP and young brood was significantly lower on day eight of the experiment ($P < 0.05$), but not on days 2, 4, 6 or 10, when compared to QMP treated colonies. The experiment was expanded in 1994 to include a queenless untreated control. The data from 1994, if consistent with the 1993 results, would indicate that the presence of young brood does act as a secondary queen signal. This signal could be in the form of a pheromone that emanates from the brood, or may act by physically allowing an outlet for nurse bees. Queen mandibular gland pheromone coupled with young brood signals apparently relay to the colony the queen's presence and fecundity. The exact origin, identification and mode of action of the brood signal remain to be determined.

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FORMATION AND MAINTENANCE OF THE HIERARCHY IN
THE QUEENLESS PONERINE ANT *DINOPONERA*
QUADRICEPS

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We studied the social hierarchy in a *Dinoponera quadriceps* colony, by analysing the different frequencies, intensities and types of agonistic behaviour occurring in the presence or absence of reproductive individuals. A colony collected in Sao Cristovao (Sergipe State) and including 24 virgin adults and brood was studied in three successive phases at the laboratory: 1) Observation of the whole colony (48 intimidation acts - antennal boxing - were recorded and two dominant individuals with ovaries in activity), 2) Individual isolation of the reproductive ants for 7 days, during which the rest of the colony was observed; 101 intimidation acts and 97 attacks (pullings and bitings) were recorded and the most aggrieved ant in the first phase became dominant (but non-reproductive), 3) Reintroduction of the reproductives, after which we observed 724 intimidation acts, 513 attacks and 158 immobilisations; the re-introduced reproductives became dominant again and the new dominant ant revealed by the second phase returned to be the most aggrieved individual. Although both reproductives were always dominant, they were aggrieved after isolation and received respectively 5% and 4% of agonistic interactions. 83% of the total time of immobilisation was turned towards the secondary reproductive, which soon died. In conclusion, an established hierarchy is maintained by relatively rare intimidation acts while the formation of a new hierarchy takes place after many intimidation acts, attacks and immobilisations which can eventually result in the death of colony members.

THE ROLE OF BEHAVIOR AND TIME IN THE REPRODUCTIVE
DIFFERENTIATION OF THE QUEENLESS ANT DINOPONERA
AUSTRALIS

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The Neotropical giant queenless ponerine *Dinoponera australis* lives in a savanna-like formation in central to southeastern Brazil, foraging singly on a variety of arthropods. Each colony has a single worker-like egg-layer and 13(\pm 6) workers (N=37). To study the aspects involved in their reproductive differentiation, 6 colonies were collected in Itirapina (22°15'S; 47°49'W) SP, Brazil. All individuals were marked prior to the behavioral observations and then dissected to record relative ovarian development, mandibular worn, and time since its emergence. The colonies are composed by 2 groups, one with relatively old workers (foragers and defenders), and another composed by callow workers and a gamergate. Most of the time the former group is involved in ritualized aggressive interactions, especially common when new workers are born. Each colony has always a dominant individual, whose ovaries are the only fully developed, but with spermatheca not necessarily filled. Most juvenile become nurses and are subordinated to the gamergate, but may dominate over one another, forming an apparent linear dominance hierarchy. Each newborn assumes always the top rank in this group, immediately below the gamergate. As it gets older it becomes gradually totally subordinated, its ovaries atrophy, and it passes to perform only activities within the nest. When the gamergate dies (or is experimentally removed) the most aggressive and youngest juvenile worker replaces it. In two colonies, however, the gamergates were attacked by members of the old workers group, in aggressive non-ritualized encounters that resulted in death or a sudden change in the former dominant status, but again a young and aggressive worker took over the egg-laying task. Reproductive differentiation in this species results not only from aggressiveness, but also by the time of the individual emergence and the colony age structure.

**DOMINANCE INTERACTIONS AND CONTROL OF
REPRODUCTION IN THE QUEENLESS ANT
GNAMPTOGENYS SP. FROM SULAWESI (PONERINAE)**

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Gnamptogenys sp. is an arboreal ponerine ant; colonies (67 ± 36 workers, $N=6$) were collected from small pre-existing cavities in the branches of various rainforest trees. This is the first queenless species discovered in this large Ectatommine genus; other species have either alate queens or ergatoid queens. Dominance interactions occur among workers, and their role in reproductive regulation was studied in colonies with marked individuals. At least one gamergate (mated egg-laying worker) was found in each colony. Their ovaries were well-developed: several yolky oocytes at different stages of maturity, distinct trophocytes, and dark yellow bodies in each ovariole. The occurrence of up to three mature oocytes per gamergate, and the monitoring of egg numbers in monogynous colonies, indicate that fecundity is relatively high for a queenless Ponerinae. The ovaries of most virgin workers exhibited limited development: ovarioles were shorter than the gamergates', often with a single small yolky oocyte at their base, and without yellow bodies. These workers were frequently observed laying distinct trophic eggs: variable in length, abnormal in shape and lacking a chorion. Trophic eggs are immediately given to the nearest larvae.

Intracolony aggression takes two forms: antennal boxing, and bite & drag. Boxing is frequent between gamergates, but very rare between gamergates and virgin workers. In unmanipulated colonies both aggressive interactions are infrequent among virgin workers, but following the removal of the gamergate, they increase dramatically. After some time a hierarchy is established and aggression decreases. We are currently testing the hypothesis that subordinate nestmates do not tolerate a virgin dominant individual in the presence of a gamergate. When a gamergate was reintroduced to a group of orphaned workers, her mere presence immediately triggered aggression towards the worker who had become dominant.

RAIDING AND MIGRATORY BEHAVIOR IN THE NEOTROPICAL TERMITE-HUNTING ANT *PACHYCONDYLA* (= *TERMITOPONE*) *MARGINATA*

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A few genera in the subfamily Ponerinae exhibit group-raiding and/or migratory behavior. These two habits are found associated in three neotropical termitophagous species of *Pachycondyla* (= *Termitopone*). This study investigates the group-raiding behavior on termite nests and the migratory habit in *Pachycondyla marginata*. Nests of *P. marginata* (N=83) were marked and followed from February 1991 to September 1993 in a semideciduous forest in Campinas, SE Brazil. A total of 202 group-raids by *P. marginata* colonies were observed, and in all cases the raided termite species was *Neocapritermes opacus* (Termitidae). Colonies of *P. marginata* (500 to 1500 workers) hunt on termite nests approximately every two weeks; group-raids can occur both day and night and may last 2 to over 24 h. Nearly 20% of the workers within a colony engage in hunting activity. Most raids are aimed at one target termite nest, but occasionally two nests can be simultaneously raided by one ant colony. The raid starts with a few ants penetrating into a termite nest, 0.12 to 38 m far. Scout ants return to their nest showing trail-laying behavior, and the whole recruiting process may last 2-4 h before a stable raiding column is formed and the first termites are retrieved. Ants carry 1-2 paralyzed termite-prey; workers and soldiers are captured in a proportion of 13:1. Nearly 1600 termites are captured during one raid. Migration by *P. marginata* colonies cover distances of 2-97 m (N=48) and may last 1-2 days. Colonies relocate their nests to greater distances during the dry season, and the approximate residence time at a given location is 150 days. Some colonies have more than one dealated female, and colony fission of one mature colony was observed once. Massive group-raiding and nomadism are considered diagnostic behavioral patterns of the "true" army-ants, Ecitoninae and Dorylinae. The predatory and migratory behaviors of *P. marginata* probably represent an early step in the evolution of the true army-ant habit.

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RESOURCE-PARTITIONING IN MALAYAN *LEPTOGENYS* SPECIES (FORMICIDAE: PONERINAE)

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Niche differentiation theory predicts that sympatric species must differ sufficiently in resource requirements in order to coexist. Seventeen species of the exclusively predatory genus *Leptogenys* were found to co-occur in a small area ($< 1 \text{ km}^2$) of a secondary tropical rain forest near Kuala Lumpur, Malaysia (Ulu Gombak Field Studies Centre). Ecological separation along 4 niche dimensions was investigated: (1) Habitat utilization, (2) systematic group of prey, (3) prey size and (4) circadian activity patterns. (1) Four strata are utilized: (a) leaf litter (11 spp.), (b) upper soil layer (3 spp.), (c) space between soil and leaf litter (1 sp.), (d) all ground layers plus lower part of vegetation (2 spp.). (2) The army ants *L. distinguenda* (Maschwitz et al. 1989), *L. borneensis*, and the group-raiding *L. diminuta* prey on a wide taxonomic range of arthropods. Other species, in contrast, are specialized largely or exclusively on a narrow range of prey, e. g. isopods, termites, or earwigs (Steghaus-Kovac & Maschwitz 1993). (3) Prey size depends on foraging strategy: Solitary foragers retrieve small prey items. The group-raiding or mass-recruiting species often capture arthropods which exceed the predators' body size. At least one army ant, *Leptogenys mutabilis*, hunts mainly termites, i. e., small, but difficult prey (Maschwitz & Steghaus-Kovac 1991). It appears, that the observed differences in habitat and prey utilization permit the long-term coexistence of many congeneric species in a relatively small area.

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THE FORAGING STRATEGY OF *FORMICA TRUNCORUM*

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Different aspects of the foraging strategy of *Formica truncorum* have been investigated in the laboratory as well as in the field. The field experiments took place in forest habitats along the southern coast of Finland. Like the other *Formica sensu stricto* species, *Formica truncorum* can develop a trunk-trail foraging strategy focusing the worker force to stable resources of food. We have demonstrated that the workers of this species develop a high degree of route fidelity also with respect to the branches of a bifurcation. Nevertheless, nests may lack obvious foraging routes, foragers dispersing all over the visited area. Even in this case, our marking experiments have demonstrated the fidelity of the workers to different sites. The workers' fidelity has been reproduced in artificial devices in the laboratory and in the field, in order to study the orienting cues. Those experiments lead to the conclusion that chemical and celestial orientation are negligible compared to visual (landmarks and/or canopy) cues. Field experiments also demonstrate that *Formica truncorum* is able to recruit nestmates to an important source of food. The directional component of this process has been analysed during laboratory experiments with Y-bridges (food in one side only). Though recruitment is clearly directional, the percentage of error is high, permitting a symmetrical exploitation when food is presented on both sides. This study has demonstrated the diversity of the foraging strategies developed by *Formica truncorum*: trunk trails, recruitment capacity, dispersal of the foragers all over the area. In this sense, it could represent an intermediary link between the genera *Serviformica* and the *Formica s.str.* species.

SOCIALITY AND POLLEN FLOW : DIRECT EVIDENCE FOR EFFECTIVE IN-HIVE POLLEN TRANSFER.

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With solitary insects, entomophilous pollination can result from the carry-over of pollen during a foraging bout, a foraging trip, or several consecutive trips. With eusocial bees, there is the added possibility that pollen be transferred among nestmates in a colony. In 1957, Karmo & Vickery suggested that, with honey bees, *Apis mellifera*, in-hive pollen transfer could lead to effective pollination. DeGrandi-Hoffman *et al.* endorsed repeatedly this hypothesis based upon indirect evidence on fruit set and seed yields, along with the observation that the haircoat of foragers carried pollen from cultivars other than the one upon which the bees were captured. The viability of this pollen was never examined, however, and a large body of results on oriented pollen dispersal in relation to the planting geometry of pollenizers go against this hypothesis. We therefore tested in-hive pollen transfer in 1993 by isolating individually 3 adjacent pistillate kiwifruit vines (*Actinidia deliciosa* var. *deliciosa*) in pollenproof cages. One cage served as control while the two others were each provided with a colony of about 8 000 honey bees in a 5-frame double-entrance hive. The two entrances were on opposite sides and at different levels, one open toward the outside and the other toward the inside of the cage. In addition, one hive was divided in the middle by a screen with 2x2 mm openings enabling only contacts between the bees of each compartment. Kiwifruit is a functionally dioecious species and the vine in the control cage did not set any fruit. All flowers hand-pollinated in each cage (10 per vine) gave a fruit with similar numbers of seeds (range 957 - 1501 seeds/fruit). Fruit set in the two cages with a double-entrance hive was low and similar (7.4%) while that on the two adjacent open-pollinated vines exceeded 90%. The 48 fruit produced on the vine enclosed with the plain double-entrance hive contained 5 to 700 seeds each (average 142 seeds/fruit), which was significantly different from the seed content of the 58 fruits harvested on the vine isolated with the double-entrance hive split in two compartments (range 2 - 146 and average 31 seeds/fruit). These is the first direct evidence that in-hive pollen transfer can result in effective pollination and that its efficiency depends upon the amount of contact between the bees. This conclusion has strong implications in terms of the scale of the gene flow associated with insect-mediated pollen flow for natural populations as well as cultivated species (transgenic plants) when the pollinator is a eusocial insect.

EXPLOITATION OF AVAILABLE RESOURCES BY BEE FAUNA (APOIDEA) AT THE PANGA ECOLOGICAL RESERVE (CERRADO), UBERLÂNDIA, M.G., BRAZIL.

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The present work was carried out in the "Panga Ecological Reserve" an area of cerrado, neotropical savanna vegetation. Surveys of flower-visiting bees were done from April/88 to April/89. The bees were collected by net sweeping. 1,226 individuals belonging to 128 species and 39 genera of 6 families of Apoidea were sampled. The Apidae family was the most abundant in number of individuals while Anthophoridae was in number of species. The data also show the dominant species of Apoidea, the frequency of this group throughout the year, and preferential foraging time of the bees on the available floral resources. *Trigona spinipes*, *Tetragonisca angustula angustula* and *Apis mellifera* (Apidae) were the frequent species in the area. Bee frequencies showed various patterns of seasonality. For example, the period in which most bees of *Trigona spinipes* were observed were July/88 and September/88 to November/88 and the preferential foraging time was variable; *Tetragonisca angustula angustula* visited flowers almost every time of the year; the most of the bees of Anthophoridae, Halictidae and Megachilidae were restricted to determined periods. Throught the analysis of dominant species of bees and plants, the relationship between them was verified, as well as the index of similarity.

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OPTIMAL PATCH USE BY WORKERS OF *LASIUS NIGER*.

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When foragers optimise their exploitation of patches of food, the optimal patch residence time is predicted by the marginal value theorem (Charnov, 1976). If foragers are presented with patches of equal quality, then the residence time that maximises the rate of energy intake will depend on the time travelling between patches. In the context of central place foragers the patch residence time will depend on the distance from the nest to the feeding patch (Orians and Pearson, 1980). This prediction was tested for a laboratory colony of *Lasius niger*. The colony was established in a linear foraging arena and fed on 10% sucrose solution. In a repeated series of experiments, the foraging workers were presented with patches of food (0.25 cm³ of 10% sucrose solution) at 1, 2 or 3 meters distance from the nest entrance. Individual workers were timed while they were feeding from the food patch. This 'patch residence time' was found to increase as the distance from the nest increases. The workers foraging behaviour thus maximises the rate of energy intake.

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COLONY-LEVEL HOMEOSTASIS IN NEST ARCHITECTURE OF *POLISTES*

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Most studies on social wasps are based on the assumption that the individual insect is the critical level of behavioral organization. General views of colony-level phenomena are few, recent and focus on nest construction. Recent computer simulations found that identical individuals that do not interact directly, and that rely upon strictly local information, can produce life-like *Polistes* nests (1), but data from live colonies suggests that even such simple aspects as nest size may be controlled at a level higher than the individual (2). In the absence of any higher function, and given our understanding of factors influencing cell initiation (3), experimental removal of both new eggs and the cells they occupy should not affect the construction rate on the nest. Such damaged nests would remain forever somewhat smaller than unmanipulated nests built by foundress cohorts of the same size. However, the construction rate on experimental nests doubled immediately, far surpassing the rate of natural colonies, and achieved the same nest size as the natural colonies that suffered no traumatic loss of cells (2). It appears that the size of the nest (and therefore the number of brood) is controlled by a property more complex than simple, classical control mechanisms. Nest size is itself a trait that has evolved some form of homeostasis. Complete understanding of construction behavior will be available only from a combination of individual and colony-level perspectives.

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CYCLICAL OLIGOGYNY AND RELATEDNESS IN
NEOTROPICAL WASPS OF THE GENUS *Parachartergus*
colobopterus BASED ON BEHAVIORAL AND GENETIC
DATA

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Cyclical oligogyny has been proposed as the mechanism for unexpectedly high relatedness found in neotropical swarm-founding wasps with multiple queens (Queller et al. 1988, 1992). In cyclical oligogyny swarm-founding nests alternate between periods of numerous queens and low brood relatedness and, after death or submission of some of the queens, periods of few queens and high brood relatedness. During the summer of 1993, eight young colonies of the neotropical wasp *Parachartergus colobopterus* from Maracay, Venezuela were marked and their behavior videotaped. The goal of this study was to determine if workers would preferentially aid closely related queens in rearing their brood or if relatedness within the colony has no effect on this behavior. The wasps were collected and subjected to genetic and morphological surveys in the lab. The videotapes were observed and different behaviors were scored (aggression, submission, and feeding). DNA was extracted from all the wasps and screened over 11 microsatellite loci. Based on the genotypes obtained for two of the eight nests, the relatedness for one was high while for the other one was low. The aggression observed in the nest with low relatedness was less than expected. These nests will be compared for the participation of the workers in rearing the brood and the worker-brood, worker-queen relatedness.

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REPLACEMENT OF THE PRIMARY QUEEN WITH NEOTENICS
IN AUSTRALIAN COPTOTERMES (ISOPTERA):
CONSEQUENCES FOR THE REPRODUCTIVE BIOLOGY OF THE
COLONY

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Colonies of Australian *Coptotermes lacteus* and *C. acinaciformis* respond to experimental orphaning, the removal of the primary queen, with the development of nymphoid neotenics, permitting the colony to resume breeding within 3 months. In one population of *C. lacteus*, neotenic-headed colonies have produced almost exclusively male nymphs (alates) over the observation period of 4.5 years (sex ratio of nymphs (alates) about even in primary-headed colonies). Orphaned colonies of *C. acinaciformis* and a second population of *C. lacteus*, studied to date for only 2 years, and one colony of *C. lacteus* orphaned from natural causes showed similarly skewed sex ratios of their nymphs (alates). As preliminary observations indicate the sex ratio is not biased at egg laying; in neotenic-derived brood 1st stage larvae and workers contain both sexes. A possible mechanism leading to the observed nymphal sex ratio could be, for example, that female larvae are prohibited from developing into nymphs but male larvae not. An alternative mechanism could be that 2nd stage larvae of both sexes have the potential to develop into nymphs, but those female individuals preparing to moult into Nymph-1 are eliminated by workers. Production of exclusively male nymphs in orphaned colonies prevents the development of further female neotenics which could compete with the breeding neotenics. Such competition should be delayed until orphaned colonies are assured of their survival. Our field observations indicate that resumption of breeding with the help of neotenics after orphaning is not a guarantee for survival of the colony. For as many years as the skewed sex ratio is maintained release of male alates only forces outbreeding. Observations from *C. formosanus* in Guangzhou, China, indicate similar responses to orphaning.

POLYGyny AND INTRACOLONIAL KIN STRUCTURE IN THE ANT *Formica japonica* MOTSCHULSKY

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Polygyny and intracolony kin structure of the ant *Formica japonica* were studied in the field and laboratory. Excavation of the nests in the study site, Gotenba, the east slope of Mt. Fuji, Japan, revealed that *F. japonica* is facultatively polygynous all the year round and the colonies tended to increase the queen number after the nuptial flight season. The multiple queens also had a tendency to be separately located even in the same nest. Moreover, dissection of queens and rearing experiments indicated that most of the queens in polygynous colonies had mated and produced diploid eggs. These suggest that the kin groups are formed around each queen. DNA fingerprinting was used to examine the intracolony kin structure in more detail. The fingerprint band patterns were apparently governed by simple genetic principles and showed that most of the queens had mated just once. The mean band sharing coefficient of DNA fingerprints among full sisters was 0.70 (S.D.=0.13), and the mean values between queens and their daughters was 0.49 (S.D.=0.11). The mean band sharing coefficients among the nestmate queens of polygynous colonies varied among the colonies (range 0.38-0.68), suggesting that polygynous colonies of *F. japonica* are not always composed of closely related kins. Comparison of DNA fingerprints of adult and pupal workers, and pupal gyenes indicated that not all queens present in nests produce equally new female broods in the same season. Moreover, gyne production may be monopolized by particular queen(s) in polygynous nests, reflecting the reproductive competition among multiple queens.

HOW DO ANTS ESTABLISH A "CEMETERY" ?

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Lasius niger workers collect dead individuals in the nest and transport them to a pile outside the nest. In this way the nest remains clean from putrefying materials. The pile consists of the corpses of colony members, the remains of insect prey and other usefullless materials. Sometimes it has an organized structure, with different objects arranged in different layers or parts of the pile.

A number of studies have been made on such necrophoric behaviour and the chemical signals used by the workers (Wilson et al., 1958; Ataya and Lenoir, 1984). Our goal is to understand the link between the individual behaviour and the global pattern formation (i.e. the dynamics of the distribution of corpses).

Experiments on *Lasius niger* using dead ants from different species and other insects reveals a series of cues which are important in the pattern formation. The corpse is deposited outside the nest and the same or another worker then transports it further from the nest hole. The dropping of the corpse is influenced by spatial irregularities, the distance from the nest hole, meeting other corpses and the chemical signals from the piles of putrefying corpses. The great number of repetitions of the picking up and the putting down of the individual corpses, associated with amplifying mechanisms, leads to the formation of the "cemetery" in this species.

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DEVELOPMENT OF THE HONEYBEE OLFACTORY SYSTEM: IDENTIFICATION OF ANTIGENES PUTATIVELY INVOLVED IN CELL-CELL INTERACTIONS DURING BEE OLFACTORY SYSTEM ONTOGENY.

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Bee olfactory system appears to be very well suited to investigate the role of genetic and epigenetic factors during olfactory development of the honeybee (Masson and Arnold 1984, Gascuel and Masson 1987). The main features of the honey bee olfactory system such as selective fasciculation defasciculation, glomeruli formation and neurite arborizations are likely to be controlled by cell-cell interactions (Gascuel and Masson 1991a and b). In order to identify the molecular basis of such mechanisms we undertaken monoclonal antibody productions and developed primary cell culture systems. On the one hand, mice were immunized with membrane fraction of bee brain of specific stages, hybridoma were generated, and those producing antibodies binding to brain cryo-sections were selected. On the other hand, long term primary cultures (Gascuel *et al.*, 1994) and co-cultures of (i) sensory neurones-antennal lobe neurones, and (ii) antennal lobe neurones-mushroom body interneurones were set up. This allow to test the function of the antigens recognised by the antibody by functional blockade. The results gained with different antibodies allow to propose an antigene-based map of the bee brain, and especially of the antennal lobe. The so-called CB11, CF5, A2B7, which putatively stain glial cells, synaptic neuropile, specific area of the mushroom body and antennal nerves, respectively, has been obtained. For these antibodies, based on their (i) patterns of expression both in the brain and cell cultures during development, (ii) membrane localisation and (iii) molecular nature, their putative role in cell-cell interaction during brain development will be discussed.

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FLIGHT METABOLIC RATES OF QUEENS AND DRONES
OF AFRICAN, EUROPEAN, AND HYBRID HONEY BEES

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As feral populations of African honey bees (*Apis mellifera scutellata*) spread throughout the neotropics, hybrid populations are initially formed with European (*Apis mellifera lingustica*) bees (Rinderer et al. 1991). However, the hybrids do not persist after the African population becomes established (Hall and Muraldiaran 1989). We have previously shown that mass-specific metabolic rates (MR) during agitated flight of African workers are greater than for European workers (Harrison and Hall 1993). In addition, MR of hybrid worker bees are low and non-intermediate. We now report that the MR of African queens during flight exceed those of European queens. MR of first generation African-European hybrid queens are low and non-intermediate. African drones also have MR above European and hybrid drones, and have higher thoracic temperatures. Among drones, first generation hybrids are intermediate in MR. These data suggest that increased MR may contribute to the spread of the African honey bee by increasing flight speeds and maneuverability of both queens and drones. In addition, the decreased MR in hybrid workers and queens may result in negative heterosis, contributing to the preservation of the African genotype during colonization of the Americas.

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HYGIENIC BEHAVIOR AND DISTRIBUTION OF OCTOPAMINE IMMUNOREACTIVE CELLS IN THE HONEY BEE BRAIN

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Hygienic behavior in *Apis mellifera* is a mechanism of resistance to disease and possibly parasitic mites. Bees that are hygienic are able to detect, uncap, and remove diseased or infested brood from the nest. We addressed the question of whether the behavior is associated with differential distributions of octopamine in the brains of hygienic and non-hygienic bees. Hygienic and non-hygienic bees of the same ages were collected from observation hives. Their brains were fixed in GPA and stained with an antibody against octopamine. The secondary antibody used was conjugated with cy-5 fluorophore for imaging on the confocal microscope. In both hygienic and non-hygienic bees the brains showed staining in the central body and in clusters of 8-10 cells in an area surrounding the esophageal foramen. In the hygienic bees, two pairs of large cells, dorsal to the antennal lobes, stained brightly. These cells were absent in the brains of non-hygienic bees. A tentative interpretation for the differences is that hygienic behavior, a stereotypical behavior, may more likely be expressed in bees that possess greater levels of octopamine. Hygienic behavior could be influenced by the release of octopamine because of its sensitizing effects on the chemosensory neurons mediating the detection of diseased or dead brood and by altering the motivational state of the bee to perform the hygienic-related motor tasks.

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DEPENDENCE OF FREE AMINO ACID LEVELS IN HONEYBEES ON SEX, AGE, PROFESSION AND DIET

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Division of labour in honey bee colonies is reflected in many physiological parameters such as protein metabolism, food consumption and utilisation, size and function of various glands, and haemolymph volume. We investigated the amino acid content of the haemolymph of both workers and drones. The content of free amino acids is about 20-fold higher than that of mammals. Proline predominates, constituting approximately one third of the total free amino acid content. In both sexes the lowest total content occurs after the switch from hive bees to flying bees (foraging activity of workers and mating flights of drones). Environment and food strongly influence amino acid levels in the haemolymph. Sister bees living in different colonies, or in cages with natural food or artificial diets such as casein and/or sucrose solution, differ in quality and quantity of haemolymph amino acids. Some of the caged groups had only 50% the amino acids of bees in the colony from which they originated (although variation amongst sister colonies could be almost as great). Nevertheless, the proline proportion remained high, indicating a physiological function for this amino acid. Whereas important functions for this amino acid have been reported for flight in other insects (Crabtree and Newsholme, 1970; Zebe and Gäde, 1993), this is not so for honeybees to date. As availability of protein changes the quantity and quality of haemolymph amino acids we suggest that a generally low amino acid haemolymph level, or reduced levels of specific amino acids, might serve as a signal for a forager bee to collect either nectar or honey.

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DISCRIMINATION OF PLANT VOLATILES IN THE HONEYBEE : COMBINED BEHAVIOURAL, ELECTROPHYSIOLOGICAL AND CHEMICAL APPROACHES

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Foraging behaviour of honeybees is dependent on learning processes involved in the perception of plant volatiles. These substances play a major role in cueing orientation to food sources. In order to investigate complex odour recognition in the honeybee, the conditioned proboscis extension responses (CPE) of individual restrained bees were studied. As this response occurs naturally when foragers land on flowers, the CPE assay is considered to be a useful tool for characterising behaviourally active plant volatiles. The bees were stimulated either by synthetic samples of oilseed rape floral volatiles, presented individually or as a mixture, or by an air entrainment extract of oilseed rape flowers. A standard CPE assay or a novel combined gas chromatography (GC)-CPE technique was employed to stimulate the bees. With both procedures, it appeared that, after training to the synthetic mixture, bees consistently responded to three components out of the six present in the mixture. When the coupling technique was extended to include the simultaneous recording of electroantennogram responses (EAG), it was shown that all six components were detected at the sensory level, whereas discrimination between components appeared at the behavioural level. Further experiments using the air entrainment extract as the stimulus in the GC-CPE system confirmed that mixture recognition relied on a limited range of compounds, with only 5 components out of 50 eluting from the GC column eliciting CPE responses in more than 35 % of the bees previously trained to the extract. The effect of prior olfactory experience on discrimination abilities was then evaluated by comparing the responses of naive (no training), conditioned (paired training to the extract) and pseudoconditioned (unpaired training) bees. CPE activity was recorded in all bees for a limited number of components of the extract. These are now being identified. Compared to the spontaneous responses of naive bees, the level of CPE activity was increased in the conditioned group and depressed in the pseudoconditioned one. These data show that recognition of complex odours is based on a limited range of key components.

**TRADE-OFF BETWEEN COMPETITIVE SUPERIORITY
AND DISPERSAL ABILITY PRODUCING SOME PECULIAR
DISTRIBUTIONAL PATTERNS IN TREMITES**

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Based on nesting system and feeding habits, the life types of termites are divided into three categories: one-piece, intermediate and separate types. A piece of wood serves one piece type as both a nesting site and food resource, whereas it serves separate type as only one of their food items. This leads to asymmetrical competition between the two types. Intermediate type nests in a piece of wood and construct galleries to consume other wood pieces as well. These three types show different biogeographical distribution. Separate type represented by Termitidae is distributed in tropical mainland, and intermediate type represented by most species of Rhinotermitidae is widely distributed from tropical to temperate regions. One piece type, which is divided into 3 sub-groups, shows marginal distribution: damp wood termites (Termopsidae) show a typical amphitropical distribution, ordinary wood termites (*Prorhinotermes* of Rhinotermitidae) are confined to tropical and subtropical islands, and dry wood termites (most species of Kalotermitidae) tend to be confined to coastal and island forests of tropical and subtropical regions. One piece type (especially dry wood and ordinary wood termites) are better colonizers across oceans than separate type, because termites usually cross oceans by rafting. This mutually exclusive distribution of one piece and separate types can be explained by the trade-off between the dominance in asymmetrical competition and that in dispersal ability across oceans.

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PHYSICO-CHEMICAL CHARACTERISTICS OF SOME SOIL- FEEDING TERMITARIA

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This study brings to light the complexity of the pedological effects of termites, in this case humivorous, and shows that their influence in function of their diet and nest-building behaviour cannot be generalised.

This study demonstrates that the species *Cubitermes fungifaber*, *Thoracotermes macrothorax*, *Procubitermes niapuensis*, *Crenetermes albotarsalis* and *Noditermes lamanianus*, by their biological activity, build nests rich in organic matter and exchangeable cations as compared to the control soils. In the nest-walls elaborated by the humivorous termite studied the carbon rate was shown to include a significant amount of humic acids, inducing fulvic acids/humic acids ratios close to 1. It can be concluded that this organic matter is more polymerised than that of control humiferous horizons.

The horizons near the nests and influenced by these termites, also show differences which enable us to estimate the extent of the effects of these termites. *C. fungifaber*, *T. macrothorax* and *C. albotarsalis* disturb their horizons upto about a depth of about 30 cm and *N. lamanianus* upto about 15 cm, while *P. niapuensis* does not seem to burrow the horizons beneath its nest. The materials built by *C. albotarsalis*, unenriched by organic matter, did not show variations in the structural stability (Is Index) when compared to the horizons of control soils.

It appears that these "efficient" species enrich their building materials with organic matter and certainly influence the stabilisation of humic acids by thoroughly mixing the plant debris with phyllitic elements of the soil in their digestive tract. In fact, we are right in thinking that the stable organo-mineral microaggregates formed by the metabolic activity of termites and then incorporated in the walls or in the humiferous zones are mineralised with difficulty, and play a beneficial role in the elaboration of the humic-clay complex of the soil, as in the case of *T. macrothorax*. From this point of view, certain humivorous termites thus have an important role to play in the organic matter cycle of the soil and contribute to its conservation. The physical properties are modified and the termitaries have a better structural stability than the control horizons. Nevertheless, this study shows that we cannot generalise these effects and ethological studies should accompany physico-chemical analyses. In fact, only a deeper ethological study of *C. albotarsalis* will help in understanding why its nutritional and building behaviour do not have the same consequences as the other genera. Similarly, observations of the feeding habit of *P. niapuensis* will unveil from where the workers get their nutritional requirement.

**TERMITES AND MOUND DWELLING MICROORGANISMS: A
SYMBIOSIS PROMOTING ORGANIC MATTER
MINERALIZATION AND NUTRIENT CYCLING**

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The microbiological activity of soil from the mounds of several termites occurring in northern Queensland, Australia, has been examined. This information is combined with the results of other studies in northern Australia in order to determine the role of microbiological activity in termite mounds. Microbial biomass carbon levels have been determined using the substrate induced respiration technique (SIR) and other microbial activity indices such as nitrifying activity and enzyme activities have also been determined. The results of these studies demonstrate that the mounds of several termite species are sites of significant microbial activity. The microbial biomass carbon levels of termite mound soils ranged from 1.5 to 6.1 times that of the nearby surface soils. Termite mound soils also showed significant nitrifying activity and peptidase and amidase activities. Inorganic nitrogen levels (NH_4^+ and NO_3^-) of the mound soils were greater than those of nearby surface soils. Experiments have shown that inorganic nitrogen is readily leached from the termite mounds, providing a plant available form of nitrogen to the ecosystem. These studies have shown that mound-building termites and the microorganisms present in the mounds together play a major role in the decomposition of organic matter and the cycling of nitrogen. It is proposed that the relationship between these two groups of organisms might be viewed as a symbiosis, with termites providing both a suitable environment and food source for microorganisms, while the microorganisms control the level of faecal derived organic material in the mounds. As a direct result of this symbiosis, termite mounds are sites of high decomposer activity and nutrient concentration and provide foci in the landscape for the redistribution of nutrients, particularly nitrogen.

DYNAMIQUE DES TERMITIERES EPIGEES D'UN BASSIN VERSANT DU NORD-OUEST DE LA COTE-D'IVOIRE: IMPACT SUR LES SOLS ET LA VEGETATION

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Caractériser les facteurs du milieu qui influent sur les couvertures pédologiques et végétales, afin de mieux comprendre le fonctionnement hydrique d'un petit bassin versant est l'objet principal du programme interdisciplinaire dans lequel nous avons travaillé. Nous y avons étudié l'impact et le rôle des termites dans le milieu: répartitions spatiales des nids épigés et évolution de ces répartitions au fil des années, en relation avec l'évolution du milieu (jachères). L'analyse montre que les corrélations entre les distributions -toutes agrégatives- des espèces ou groupes d'espèces peuvent changer selon les parcelles et les années. En fonction des niveaux de probabilités, la distribution des nids de *Cubitermes* spp. et de *Trinervitermes* spp. montrent dans l'ensemble des corrélations positives. Une corrélation négative est par contre observée entre les distributions des nids de *Cubitermes* et de *Macrotermes bellicosus*. L'étude de la dynamique de ces nids épigés a montré d'importantes fluctuations d'effectifs d'une année sur l'autre pour *Cubitermes* et surtout pour *Trinervitermes*; phénomène lié au caractère polycalique des derniers. Ceux de *M. bellicosus*, en particulier les nids en activité, présentent également d'importantes variations: 3 à 7/ha. Une véritable "pullulation" de jeunes nids est observée certaines années, suivie d'une mortalité très élevée. Une des conclusions essentielles est le turn-over extrêmement rapide des populations de termitières épigées, y compris celles de grandes tailles comme *M. bellicosus*. Ce renouvellement s'accompagne d'une croissance rapide des nids, notamment les plus jeunes, concomitante d'une érosion plus ou moins rapide des nids morts. Cet apport de matériau néogène, de composition différente de celui à la surface du sol, a des impacts divers sur les couvertures pédologiques et donc sur la végétation du bassin versant.

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ECOLOGY OF TWO ARBOREAL-NESTING TERMITES IN NEW GUINEA COCONUT PLANTATIONS

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We studied the factors affecting the distribution and abundance of arboreal-nesting termites in coconut plantations. In these homogeneous biotopes, the dynamics of colonization, the effect of the environment and the interactions between colonies can be easily observed. The two most abundant species in this habitat are *Microcerotermes biroi* (present on 80% of the trees supporting termite nests or covered runways) and *Nasutitermes princeps* (14%). *M. biroi* is usually monogynous (79% of the colonies) and reproduces through massive swarming flights. Colonies may be polydomous and colonize 1-5 trees; sometimes, several colonies are built on the same tree. *M. biroi* appears to be a pioneer species: this species was first to invade a young, 10-year old coconut plantation; within 3 years, 40% of the trees had been colonized. By contrast, *N. princeps* is often polygynous (60% of the colonies), which suggests that reproduction by budding is common in this species. Colonies are often polydomous and colonize up to 20 trees covering a large territory, of up to 1000 m². An exceptionally large, presumably unicolonial system featuring 134 nests on 3.1 ha was discovered. The plantation structure affects the colonization by arboreal termites: in clear plantations of tall trees (<100 trees/ha, ~25m high), 25% of the trees are colonized by termites, whereas this proportion doubles in denser habitats (120-300 trees/ha, trees >13m high). Furthermore, nest volume tends to increase with habitat density. Predation by ants is limited: arboreal *Crematogaster* spp. interfere only locally. Interspecific competition is conspicuous: *N. princeps* outcompetes *M. biroi* and invades its nests. Intraspecific competition has milder consequences, since when trails of agonistic colonies meet, they tend to diverge afterwards. In conclusion, the two species use different strategies: *M. biroi* invests in alate production to colonize the habitat rapidly by numerous small colonies, whereas *N. princeps* develops large colonies which can produce buds and rely on offensive mechanisms to expand its territory in an environment already largely occupied by *M. biroi*. Habitat structure and interspecific competition seem the two most important factors affecting the arboreal-nesting termites in coconut plantations.

**ALARM INSIDE THE BEEHIVE !
HONEYBEE WORKERS STING SHEATHS :
PHEROMONAL AND PROTEIN SECRETIONS**

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Following a disturbance of a bee colony, the guardians extrude their sting apparatus and expose their stinger, its sheaths, the setaceous membrane and emit an alarm pheromone. The Koschewnikow glands seem to produce and secrete the alarm pheromone on the surface of the setaceous membrane.

HOWEVER:

A.- Bioassays have revealed that of all components of the sting apparatus, the sting sheaths released the highest level of aggressive behaviour in workers bees (alarm, attraction, and stinging) as follows:

Sting apparatus > sting sheaths > setaceous membrane > venom gland > venom > Koschewnikow glands > Dufour gland.

The alarm pheromone blend consists of about 40 components.

B.- Fine structural analysis shows that the median and proximal parts of the sting sheaths have the features of an exocrine gland: porous cuticle, hypertrophied epithelial cells secreting an electron dense secretory product. The protein fraction of the secretory product embedded the bristles and should allows a controlled release of the alarm pheromone. Secretion characteristics do not concern the setaceous membrane

So, Koschewnikow gland-setaceous membrane complex and the sheaths of the sting act synergistically to trigger the alarm behaviour.

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CHARACTERIZATION OF A HONEY BEE BROOD PHEROMONE

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Adult honey bee workers perform many necessary complex parental behaviors according to the age and the caste of the brood. The knowledge of the basic mechanisms of chemical ecology is fundamental to explain larval caste and age as well as kin-larval recognition by workers. There is evidence for a brood pheromone indicating presence and state of the larvae in the cells. Since a blend of ten fatty acid esters has been identified on honey bee larvae, four of them was characterized as a brood pheromone triggering the capping of the cells by the workers. Chemical analysis, using gas chromatography and gas chromatography - mass spectrometry, was performed to find out that the blend of esters vary in quantity and in proportion of each of the compounds as a function of the brood age and caste. Different behavioral tests were performed in natural conditions using larval and pupal lures made of paraffin including the compounds. The lures released an amount of esters similar to the amount naturally found on the larval cuticle. We could find out that the workers recognize the young and the old worker larvae because of the different blend of esters they produce. Modulation in quantities and in proportions of each ester as a function of age represents a chemical signature of old or young larvae for the workers. These compounds are present on the queen pupal cuticle, and three of them are involved in the recognition and acceptance, by the workers, of queen cells containing a pupa. Some of these esters can also modulate the feeding behavior of the workers to the larvae. More, the blend can also act, in experimental conditions, on the development of the hypopharyngeal glands of the workers and is involved in the inhibition of the queenless worker ovaries. Thus, the brood pheromone, made of these esters, should be considered as a major component in the chemical ecology regulating honey bee society.

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WORKER HONEY BEES (*Apis mellifera*) THAT ARE HIGH AND LOW RESPONDING TO QUEEN MANDIBULAR GLAND PHEROMONE

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A blend of five compounds known as queen mandibular gland pheromone (QMP) elicits retinue behavior, is attractive to swarms, stimulates pollen foraging, elicits short-term inhibition of queen rearing, calms queenless workers, and attracts foragers to flowering berry crops. High responding workers contact a glass pseudo-queen lure spotted with the average amount of QMP found on a queen's body up to 18 times more than low responding workers in a laboratory bioassay. Retinue response to QMP has been demonstrated to be heritable in a closed circular mating design, utilizing instrumental insemination. The retinue response to QMP has seasonal and genetic components with no correlation to the amount of pheromone found in queen glands (Pankiw et al. 1994). QMP response does not confer queen attendance behavior, nor are high QMP responding lines of worker bees stimulated with supplemental QMP to forage more than low QMP lines. However, in colonies treated with supplemental QMP, onset of foraging was delayed compared to untreated control colonies containing individually number tagged high, low and "wild" type QMP retinue responding workers. The primer effect of QMP acts to delay foraging ontogeny of workers regardless of laboratory retinue response to QMP.

Pankiw, T., M.L. Winston, K.N. Slessor, 1994. Variation in worker response to honey bee (*Apis mellifera* L.) queen mandibular pheromone. *J. Insect Behav.* 7(1): 1-15.

BROOD ATTRACTIVITY OF THE ATTINE ANT

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Discrimination and recognition form the basis of the structure of ant societies. Brood recognition is fundamental in these societies. This study investigates the capacity of *Acromyrmex subterraneus subterraneus* workers to recognize nest mates or non-nestmates in the laboratory and in the field. The different behavioural steps leading from discovery to transport to the colony of objects encountered outside the nest are used to characterize chemical signals involved in recognition by workers. Tests were performed with larvae and pupae either homospecific (from other nests); heterospecific; homospecific (from their own nests; frozen and washed with pentane) and artificial baits (with cuticular larval extracts or solvent as the control). The laboratory bioassays were conducted as follows : 1) offering larvae and pupae in the nest area; 2) offering brood and artificial baits in the foraging area. In the nest area the workers can discriminate exactly between the nestmates and non-nestmates. On average, 90% of homocolonial brood items were readily picked up and carried them back to the fungus garden. The alien brood were always rejected. This contrasts with the tests in the foraging area and field bioassays : workers cannot tell the brood apart. All kinds of larvae, pupae and impregnated artificial baits extracts were carried to the nest. Worker castes behaved differently and had different capacities for brood discrimination.

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TERMITES AND DODECATRIENOL

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(3Z,6Z,8E)-3,6,8-dodecatrien-1-ol [(Z,Z,E)-DTE-OH], one of the 8 isomers of the unsaturated alcohol, dodecatrien-1-ol, is a natural substance present in wood decayed by the fungus *Gloeophyllum trabeum*. It also has been identified as the trail pheromone of several species of American and Japanese Rhinotermitidae (Matsumura *et al.* 1968, Tokoro *et al.* 1989, 1991) and as the sex pheromone of a higher fungus-growing termite, *Pseudacanthotermes spiniger* (Bordereau *et al.*, 1991). New investigations have confirmed the key role of this substance in the biology of termites. In *Reticulitermes santonensis*, collected in western France, [(Z,Z,E)-DTE-OH] was identified by GC-MS not only in workers where it acts as a trail-following pheromone, but also in alates where it elicits sex attraction for males. In the African termite, *P. spiniger*, [(Z,Z,E)-DTE-OH] was also shown by GC-MS to be present in workers and to elicit trail following at very low concentrations. The same results were obtained in a closely related sympatric species, *P. militaris*. Thus, in several species, [(Z,Z,E)-DTE-OH] can be used both as a trail-following pheromone and as a sex pheromone. This functional duality depends on the one hand on the quantity of synthesized [(Z,Z,E)-DTE-OH], and on the other hand on the differential caste sensibility to [(Z,Z,E)-DTE-OH], especially for high concentrations which induce attraction and excitation in male alates, but inhibit trail-following behavior in neuters. [(Z,Z,E)-DTE-OH] was also very active in eliciting trail following in *Nasutitermes lujae*. Although [(Z,Z,E)-DTE-OH] could not be detected in worker extracts, chemical investigations strongly suggest that the trail-following pheromone of this highly evolved species is very similar.

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GROUP-LIVING REDUCES RISK OF PREDATION IN THE
SOCIAL SPIDER STEGODYPHUS DUMICOLA IN NAMIBIA

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Permanent group-living has many consequences for spiders. Although the mechanisms have been examined, the fundamental ecological reasons why some spiders extend mutual tolerance into adulthood remains a debated subject. In Namibia, the non-territorial permanent-social spider Stegodyphus dumicola (Eresidae) has many enemies. I examined the hypothesis that group-living S. dumicola experience lower predation risk than solitary emigrants do. Arboreal ants were the most serious enemy that raided prey remains, spider carcasses and eggs. All spiders left their retreats during ant raids. Groups of spiders kept ants at bay by laying copious amounts of cribellar silk in the path of ants. Solitary spiders were less capable of sustaining such resistance and seldom emigrated alone in regions and years of high ant activity. Nonetheless, some emigration occurs in a risk-sensitive manner perhaps because the ability of persistent ants to eventually eliminate even the largest spider colonies favours dispersers that reach temporarily ant-free sites. I conclude that, as a result of ant activities, S. dumicola are challenged at the group level, have reduced dispersal, and experience differential survival of groups.

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THE LIFE STYLE OF *CANTHON CYANELLUS CYANELLUS*, A
SUBSOCIAL NECROPHAGOUS BALL-ROLLER BEETLE.

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Field observations and laboratory experiments were carried out to analyze the subsocial behaviour of *Canthon cyanellus cyanellus*, a necrophagous ball-roller beetle from the tropical rain forests of the Mexican neotropic. The effects of some factors on the reproductive success of this species were studied. The number of eggs and survivorship of larvae to adult emergence were greater in females that nested young (11 to 15 days old after emergence) than in females that began to nest old when older (more than 30 days old). The reproductive success of the females increased with food of high nutritional quality (13.5% of proteins and 1.6% of fat) and decreased with food of low nutritional quality (5.7% proteins, 24% fat). Females supplied with food at irregular or regular time intervals had similar reproductive success, suggesting the adaptation of the females to a rich and unpredictable food resource. The behavior of immature adults was studied and separated into three phases. During phase I (1 to 5 days old), the intra- and intersexual fights for food were frequent and the scarabs rolled balls alone or stole them from other individuals or couples. In phase II (6-10 days) the joint rolling of the balls began, but the couples were unstable and sometimes reverted to individual rolling. Cooperative rolling was the most important activity of the couple in phase III with fights being exclusively intrasexual. Females were attracted to food balls rolled by mature males but not to those rolled by immature males. It likely that the food balls are impregnated with abdominal secretions during rolling and the chemical labelling of the food balls is a means of attracting a female over short distances. The balls rolled by males also repel *Calliphora* flies that compete for food with *C. cyanellus* in the rain forest. In the field males were observed to attract females by volatile sexual pheromones, but this was not demonstrated in the laboratory. Finally, the behavior of the couple in the nest was analyzed. The mechanism with which this species makes a nest with several brood balls (compound nest) was studied. In the field and in the laboratory it was found that the couple makes a food ball, 14 mm in diameter, which is cut into 2 or 3 brood balls in the nest. Survival of offspring cared for by parents was higher than for offspring without parental care. The latter were immediately attacked by fungi which prevent larval development. The propensity for food to be contaminated with soil fungi during the earlier larval stages is a selective pressure which favors parental care in this species.

**INTRASPECIFIC POLLEN ROBBERY AS A POSSIBLE
FACTOR IN SELECTING FOR SOCIAL NESTING IN
EXONEURA BICOLOR.**

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The role of intraspecific competition in the evolution of social behaviour in allodapine bees has received little attention. This report presents evidence showing that females from a heathland population of the Australian allodapine bee, *Exoneura bicolor*, will enter the nests of other females and steal pollen. Allodapine bees are unique among bee taxa in progressively provisioning brood in a communal chamber; brood are not protected by cell partitions. Pollen is stored in the nest as pollen balls, and is easily accessible to adults. The foraging activity of females from a heathland population was observed during the summers 1992/93 and 1993/94. During these periods it was noted that some females appeared to steal pollen from the nests of other females. Intrusion by foreign females was resisted by guards blocking the nest entrance. Intruders used force to get past the guard and gain entry. Apparent robbers frequently flew from nest entrance to nest entrance, antennating the openings and, if a guard were not present, entering the nest for up to 30 seconds. It is postulated that invading females are looking for pollen to steal. Egg-dumping could also occur, but was not observed. Social nests in the montane population raise more brood per female than solitary nests (Schwarz 1988). Schwarz and O'Keefe (1991) suggested that this may be because multifemale colonies are able to have a full time guard, preventing the loss of brood through ant predation. In more than 70 hours of my observations of heathland colonies, I only noted potential ant attack on two occasions, but in 40+ hours of observations where movements of conspecifics was noted, I saw more than 10 incidences of pollen robbery. It is suggested that in this population, pollen thieves and possibly egg-dumping pose a greater threat to successfully raising brood than ant attack; and that cooperative nesting may increase defence against robbers.

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**GENETIC AND ECOLOGICAL DETERMINANTS OF
SOCIAL EVOLUTION IN THE LEPIDOPTERA: LESSONS
FROM THE EASTERN TENT CATERPILLAR,
MALACOSOMA AMERICANUM.**

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Social evolution is influenced by the interplay of genetically- and ecologically-mediated factors bearing on the costs and benefits of association and cooperation. Although the magnitude of these factors is difficult to quantify, their relative importance may be inferred empirically for particular species. We assessed genetic and ecological factors of potential importance to the eastern tent caterpillar, *Malacosoma americanum*, to better understand the likely mode of social evolution in this species. We employed multilocus genetic data to assess spatial and temporal patterns of relatedness in eastern tent caterpillar colonies and obtained information on: (1) patterns of mating and sperm utilization, and (2) behavioral and stochastic factors influencing colony family structure. We found high post-eclosion relatedness in colonies, stemming from low mating frequency and biased sperm utilization. Relatedness declined as larvae developed and stochastically mixed with other colonies on the same hostplant. Ultimately, however, relatively high relatedness prevailed due to initially high intracolony relatedness values and low colony density on trees, minimizing mixing opportunities; indirect fitness contributions were thus found to be potentially significant. The genetic data are compared with ecological data for colony survivorship and resource use. We identified an early-instar window of high mortality, after which survivorship increases dramatically. Group size may influence survivorship through effects on colony establishment and foraging. These ecological factors may result in a tradeoff with genetic factors insofar as group size is increased by adjacent oviposition or colony merging. Thus, ecological forces may necessitate a relaxation of "genetic stringency" in this species such that aggregation and cooperation is favored regardless of genetic relationships between interactants; at the same time, any non-zero relatedness value increases indirect fitness and makes social behavior all the more beneficial.

SOCIAL REGULATION OF LARVAL DEVELOPMENT AND
DIAPOUSE BY THE WORKER ANTS

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The workers of the ant *Myrmica rubra* L. have been found to control effectively larval development and queen oviposition during the photoperiodic induction and termination of the diapause (Kipyatkov, 1976). When the ants maintained at short days for several weeks feed larvae and queens they force them to enter diapause. On the contrary, the workers reactivated by 2-3 weeks action of the long days or taken just after hibernation (i.e. cold reactivation) cause the resumption of larval development and queen oviposition even under the short days. We have studied this phenomenon in several ant species distinguished from *Myrmica* by the absence of the photoperiodic regulation of larval development. The most thoroughly investigated species are *Camponotus herculeanus* L. and *C. japonicus* Mayr; some experiments were also accomplished with the species of *Acantholepis*, *Leptothorax*, *Plagiolepis*, *Tapinoma* and *Tetramorium*. The experimental procedure was always as follows. Ants with diapausing larvae were maintained in a refrigerator for 3-4 months. After this artificial hibernation they were transferred to the optimal temperature regime where they have a possibility for full summer development. When the newly developed larvae in the ant groups have entered diapause at the end of the summer portion of the colony annual cycle the main part of experiment began. We realized an exchange of larvae between the diapausing ant groups having been in the "autumn state" and the groups just after the hibernation in a refrigerator, i.e. having been in the "spring state". The results of these exchanges were always the same: the nonhibernated diapausing larvae fed by reactivated spring workers rapidly developed and pupated within a short period whereas the overwintered larvae placed into the nests with autumn workers did not develop and pupate at all or only a few of them pupated sometimes. Thus, the workers of these species execute a strong control over the development and the diapause of their larvae. We can suppose this regulation is realized by means of a pheromone or a tactile stimulation of larvae by the workers as it was shown in *Myrmica rubra* (Kipyatkov, 1988; Kipyatkov, Lopatina, 1990).

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On life and death - decisions in caste-specific development of larval honey bee ovaries

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The adult honey bee ovary is highly dimorphic guaranteeing high fertility of the queen and near sterility of the worker caste. These caste differences become established in the fifth larval instar only. Prior to this instar, the developing queen and worker gonads are of the same size, and both contain 100 and more ovariole primordia. During the fifth instar, the worker ovary stops growing and the number of ovarioles is reduced to 4-7., whereas in queens practically all ovarioles are retained during metamorphosis. Analyses of the developmental programs of the queen and worker ovary should, therefore, improve our understanding on the establishment of reproductive dominance. A comparative ultrastructural analysis revealed that morphological divergence commences shortly after the last larval molt. Between 10-20 h after this molt, queen ovarioles showed formation of polyfusomes and ring channels, the typical elements of a meroistic ovary. Such extensive intercellular bridges were not formed in workers, and shortly afterwards clear signs of degeneration were observed. Formation of intercellular bridges, thus, appears to prevent cell death. On the molecular level, we analyzed protein synthesis patterns in the developing ovaries. Despite drastic differences in total protein synthesis rates, translation patterns visualized by fluorographies of one- and two-dimensional electropherograms showed considerable constancy. The only caste-specific difference was noted in a temporal shift in the synthesis of a 24 and a 29 kDa protein. As developmental hormones, in particular juvenile hormone (JH), are thought to control caste differentiation we tested their effects on the larval ovary in our in vitro system. JH did not produce any alterations in ovarian protein synthesis. In contrast, makisterone A specifically reduced translation of the 24 and 29 kDa polypeptides in a manner precisely corresponding to the in vivo situation. These in vitro analyses, thus established a clearly defined mode of action of ecdysteroids in ovary differentiation. The morphogenetic action of JH, despite of it generally being considered as a potent inducer of queen differentiation, remains elusive. Perhaps its function lies in directing organization of cytoskeletal elements during ring channel formation in queen larvae. Low JH titers, as observed in workers, may be insufficient for this process, and thus lead to initiation of a physiological cell death program.

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MULTIPLE SEX CHROMOSOMES MECHANISM IN A NEOTROPICAL SPECIES OF KALOTERMITIDAE (ISOPTERA)

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A Neotropical species of Kalotermitidae belonging to *Neotermes* (the species is not identified) has the most complex system of multiples sex chromosomes until now studied. Male first meiosis analysis revealed two linear chains of chromosomes, one of them with 30 chromosomes (designed A) and other with 13 chromosomes (designed B). One ring (or chain) with six chromosomes is also seen, but only autosomes are included in this structure. Only 8 chromosomes are excluded of the translocation complex that form 4 bivalents. In order to understand the evolutive paths of this complex it is necessary to admit that a series of translocations took place in the chromosomal evolution of the species that involved Y-autosomes, autosomes-autosomes (reciprocal translocations) and Y-Y or X-X (centric fusion). Only another species of the same genus - *N. fulvescens* has two permanent chains that involves sex chromosomes and autosomes by translocations. The male first meiosis of this species showed a chain with 9 (A) and other with 7 (B) plus 12 autosomal bivalents with diploid number of 40 for male and 42 for female. The karyotype analysis for both male and female showed that the complex of translocations is restricted to the male.

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SOCIAL ORGANIZATION OF THE BUMBLEBEES (HYMENOPTERA, APIDAE, BOMBUS) IN THE ARCTIC (WRANGEL ISLAND)

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Bumblebees is known as the only eusocial insects well adapted to the arctic environment. In 1987-89 the bumblebee ecology and sociobiology were studied in the arctic tundra of Wrangel Island (718NL, 1808EL). Predominant *Bombus lapponicus glacialis* (Sp.-Schn.) and the rarer *B. polaris* Curt. live here mainly in the abandoned lemmings' burrows and sometimes in wooden house walls or on the ground. They have small colonies with the worker caste developing during a very short (June-August) and extremely cold (the average air temperature of July is only 3.18°C) vegetation period. Sometimes the queens of the workerless *B. hyperboreus* Schonh. usurp the nests of these species. Perhaps, *B. hyperboreus* is able to nest independently as well (we observed two queens of this species with pollen loads). From 8 to 29 workers (on average 13.3) completed their development in all *B. l. glacialis* colonies ($N = 32$) studied, from 1 to 13 females (5.1) in 57% of nests and from 1 to 19 males (7.8) in 70% nests. Colonies were developing during 50-70 days. Only 37% of them had the castes of workers, females and males together in a proportion of 3:1:2. In the majority of colonies the comb included 3-4 broods (rarely two or 5-9, if the workers produced unfertilized eggs). Queens produced up to 63 eggs (on average 35.7) but only 65% of eggs (predominately of the first-third broods) developed to imago. In the beginning of August 52% of colonies had yet female and male larvae and pupae but the development ceased and all brood died out. In 10% of colonies reproductives did not develop at all. The first 5-13 workers (on average 10.8) emerged from the cocoons of the first brood in the beginning or the middle of July and had great differences in body weight (from 70 to 213 mg) because of the variation in larval feeding. The larger workers began foraging in 1-2 days after emerging and did it together with queens till the development of colonies was completed. Small workers carried out intranest works. For example, they built up from 3 to 22 (on average 10.6) honey pots. Empty cocoons and wax pockets on brood comb were used by workers for the honey storage. Pollen was stocked in the empty cocoons only. Next workers, young females and males emerged from the second-fourth broods from the middle of July till the beginning of August. Fertilized queens hid to hibernate before the middle of August. Deficit of appropriate nest sites is one of the main causes of frequent queen changes (usurpation) observed in colonies. The same ecological factor also results in the perennial use of the same burrows by bumblebees for nesting and in the utilization of nontypical refuges by queens and aggregative nesting in them.

SOCIAL RESILIENCE IN ANT COLONIES

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This paper discusses the finding that the spatial and social order of individuals in social insect colonies is re-established after colony dissociation (Sendova-Franks and Franks 1994). The individually marked workers in each of three colonies of the ant Leptothorax unifasciatus (Latr.) not only remained faithful to particular positions within their nest (Sendova-Franks and Franks 1993), but they also quickly readopted these positions relative to one another after their colony emigrated to an entirely new nest site. The additional removal of 1/3 of the workers before such an emigration did not prevent the remaining nestmates from re-establishing their positions relative to one another. The brood pattern (Franks and Sendova-Franks 1992) does not appear essential to this phenomenon either, because when almost all of the brood was removed the workers still managed to reconstruct their spatial order after emigrating to a new nest site. This phenomenon, which we term social resilience, cannot be explained by an association between the age of workers and their spatial positions in the colony. As demonstrated by the observation of another three colonies over a period of six months, workers change their spatial positions out of synchrony and different age cohorts eventually intermingle. Social resilience has implications for the role of learning in the maintenance of an efficient division of labour (Tofts and Franks 1992; Franks and Tofts 1994) to which, in part, the great ecological success of social insects has been attributed.

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MAGNETIC SENSITIVITY IN ANTS

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Although it has been demonstrated (Lindauer and Martin, 1968, Gould et al., 1978, Gould 1980) that honeybees respond to magnetic fields, evidence for a similar sensitivity in ants has proved elusive. This paper reports investigations on the ability of *Formica rufa* workers to orientate with the aid of magnetic fields in the laboratory. Experiments were carried out in the apparatus designed to exclude all other possible orientational cues than magnetism. The ability of ants to orientate under the normal local geomagnetic field and an artificial field of equivalent strength orientated at 90° to it was tested. The results provide the first unequivocal evidence of a strong magnetic compass response in ants. Furthermore, this study demonstrates that ants are able to utilise directional information from fields of geomagnetic strength.

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OPTIMAL AND REAL FORAGING IN BUMBLEBEES

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Everybody remembers the optimal foraging theory boom in 1970-1980. Then the interest to this problem decreased and nearly disappeared after the spiteful article of B. Heinrich (1983): after many years of theoretical discussions all came to the ordinary conclusion that bumblebees must conduct optimization of their behaviour to survive. But this is the goal of any adaptation and the aim of every living creature - to stay alive. At the same time the real foraging of bumblebees did not attract much attention of the researchers. The only thing that provoked several studies was the floral specialization of different bumblebee species. In this field the non-sensational results were obtained as well: the bumblebees prefer to forage on the flowers the depth of which is close to the length of their proboscis. Surprisingly nobody was interested in what is the real foraging process. The results of my 12-years investigations under the field conditions let me make the following conclusions. (1) Bumblebees have two strategies - individual and collective foraging. (2) Individual foraging can be residential and transit; these two ways of working differ in the trace patterns and in the flower handling technique (the number of inflorescences and florets visited); the residential bees have the steady territories and the spacial parameters of these individual foraging spots show sufficient stability. (3) The collective foraging (which can be only residential) displays the stability of the territories and of the sets of foraging bees; sometimes one foraging group can consequently replace another one. (4) The tendency for the attraction of the long-proboscis species of bumblebees to the short-proboscis ones while foraging has been found as well. (5) There were no species-specific peculiarities in foraging patterns in all eight bumblebees species examined under the monoflorous resource. (6) The weather conditions have only modifying influence on the above mentioned processes. The knowledge of all these special features of the real bumblebee foraging gave us the opportunity to design the broad-scale system of measures directed to the optimization of the foraging environment for the purposes of sustainable agriculture, forestry, greenery (in rural and urban landscapes) and for the conservation and protection of bumblebee populations.

FORAGING MOVEMENTS AND FLOWER DISTRIBUTION :
THE CASE OF *BOMBUS HORTORUM* (SCOPOLI)
WORKERS COLLECTING ON *DIGITALIS LUTEA* L.

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Movement patterns of collecting Apoids are known to be correlated to nectar richness or predictability. For instance *Bombus terrestris* workers (Heinrich 1979) show more directionality and longer inter-head flights when nectar reward is low. These movement rules maximize foraging efficiency by avoiding to stay in a non-rewarding zone. On the other hand, little is known about the influence of flower distribution on foraging movements. Ginsberg (1986), using experimental arrays of flowers, has shown the existence of such a relation in *Apis mellifera* L. but it remained to be confirmed in the field and for other species. *B. hortorum* workers have been observed collecting nectar on *D. lutea* on summers 92 and 93 in a chalk grassland area near Treignes (Belgium). Foraging parameters such as flight distance and turn angle were measured. The distribution of the *D. lutea* plants was assessed by measuring the nearest neighbour distance and the angle formed by triplets of nearest neighbour inflorescences. Our results show that the foraging parameters of *B. hortorum* significantly match the distribution of its resource. Notably, if *B. hortorum* exhibited an overall directionality while foraging, there were more turns in the 30-60° range than expected. Such a turn angle allows the bee to cover the shortest distance in the *D. lutea* Patch, thus enhancing foraging efficiency. Our results indicate that bumblebees can base foraging decisions on flower distribution.

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**BUMBLEBEE FORAGING: IS THERE A RESOURCE
PARTITIONING WITH APIS MELLIFERA L. BASED ON
POLLEN STEROLIC FRACTION ?**

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Bumblebee species do not use the same flower resources as *Apis mellifera* L. To test possible dietetic differences, the authors have determined the sterol compositions of pollens from several plants exclusively or mainly consumed by bumblebees: *Arbutus unedo*, *Salpichroa origanifolia*, *Cerinth minor*, *Aconitum vulparia*. For *Arbutus*, the amino-acid composition has also been determined.

Arbutus unedo provides the only food resource for a huge winter generation of S-France *Bombus terrestris* (L.) (Rasmont, 1985). It may therefore be assumed that the food requirements of *B. terrestris* are at least satisfactorily met. *Apis mellifera* also forage on this plant, though only for nectar. The amino-acid composition of this pollen nearly fits the honey-bee basic requirements determined by De Groot (1953). It is therefore astounding that honey-bees do not at all forage on *Arbutus* for pollen, despite of its correct amino-acid balance and the lack of other winter resources. *Arbutus* pollen shows a great proportion of β -sitosterol and δ 5-avenasterol and a very low one of 24-methylene-cholesterol. The latter is known as essential for *Apis mellifera* (Herbert et al., 1980; Svoboda & Feldlaufer, 1991).

Salpichroa origanifolia sterols contains great percentages of β -sitosterol, δ 5-avenasterol and also 24-methylene-cholesterol. This pollen is able to support an entire *Bombus terrestris* generation but (thanks to the 24-methylene-cholesterol?) it is also foraged by *Apis*. *Cerinth minor* entirely supports the bumblebee *Bombus brodmannicus delmasi* (Tkalcù). *Aconitum vulparia* supports populations of *B. gerstaeckeri* (Morawitz). Both plant species have pollen specially rich in δ 5-avenasterol and in 24-methylene cholesterol.

As β -sitosterol and δ 5-avenasterol are not included in the metabolic pathways of sterols in *Apis mellifera* (l.c.), the authors suggest that sterolic basic requirements of *Bombus terrestris* are significantly different. Food plants of other bumblebee species as *B. brodmannicus* and *B. gerstaeckeri* seem to share a high concentration in δ 5-avenasterol.

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THE FORAGING ACTIVITY OF SUBTERRANEAN TERMITES IN A DESERT ZONE OF PAKISTAN

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Since no information was available on the foraging activity of desert termites, an uncultivated plot of 486 m² was selected in the desert area (Bahawalnagar) for this purpose. Toilet rolls were used to study the foraging activity. Four species of termites, namely, Microtermes obesi, M. mycophagus, Eremotermes paradoxalis and E. neoparadoxalis were recorded foraging on the toilet rolls. M. mycophagus with 41.04% frequency of occurrence was more abundant and was designated as the desert termite of Pakistan. The highest number of termites per roll (73.25) belonging to M. mycophagus were recorded on November 2, 1992 at 34 C temperature (morning time) and 60% relative humidity, just after the lapse of summer season. Intergeneric and not intrageneric competition was noticed. Maximum mixed infestation was noticed in November when 15 out of 40 rolls were harbouring M. mycophagus and E. paradoxalis. The Correlation coefficient between population density/foraging activity and relative humidity was positive but extremely weak ($r=0.105$; $df, 10$; $p > 0.05$) and with temperature it was negative ($r= -0.487$; $df, 10$; $p > 0.05$). It appeared as if some critical combination of temperature and relative humidity was monitoring the foraging activity. Particle size analysis of galleries of termites on toilet rolls showed considerable enrichment in clay (22% clay; 22% silt and 56% sand), relative to the adjoining soil (1% clay 5% silt and 94% sand). There was increase in organic matter in termite constructed galleries (0.37), relative to the adjoining sandy soil (0.034); but decrease in bulk density (1.48 gm/cm³ vs. 1.55 of adjoining soil).

WINTER COLONY POPULATIONS OF AN AUSTRALIAN SWARM-FOUNDING *ROPALIDIA* ON THE TROPICAL HIGHLAND

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Polistine wasps fall into two groups with respect to the mode of colony foundation and associated social organizations: independent and swarm founders. The swarm founding, having evolved from something like an independent founding, usually associates perennial colonies with multiple queens (=egg laying females). Atherton Tableland in northeastern Australia is a tropical highland (altitude ca. 750 m) and has a cool winter season where they sometimes experience even frost. A swarm-founding polistine, *Ropalidia romandi*, is the most abundant among social wasps on the tableland, and it manages large, perennial colonies there. Adult and immature populations of 33 colonies were examined in January through June. Sizes of the colonies examined ranged from 300 to 126,000 in the cell number and from 290 to 46,500 in the female population. General features of winter colonies (those examined in the period from late April to June) are the followings: (1) the proportions of empty cells to the total number of cells is usually larger than 90%, the value being much larger than that of summer colonies (examined in January through March; 3-70%); (2) most winter colonies have a small number of larvae and/or pupae (in most cases, less than 5% of total cells is occupied by larvae and/or pupae); (3) adult females consist of a smaller proportion of queens than those of summer colonies. Another point characteristic to the winter colonies is the frequent deposition of honey drops in cells. These observations suggest that *R. romandi* in the area where more or less distinct seasons are present practices something similar to the hibernation found in temperate *Apis* bees.

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NEST RECONSTRUCTION, ABSCONDING SWARMING AND BIVOLTINISM IN THE SUBTROPICAL PAPER WASP, *ROPALIDIA FASCIATA*

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After a strong typhoon which hit Okinawa on 2 to 3 September, 1993, 35 of 61 nests destructed or fallen down by the typhoon were rapidly reconstructed by groups (sometimes more than 50) of females, and the reconstructed nests produced 51.3 ± 26.8 adults as compared with 120 ± 62.2 of undestructed nests. Although most of foundresses had been marked in spring, only one marked foundress was found on one of the 35 reconstructed nests, and as the survival rate of marked foundresses by the end of August (5 months after nest-foundation) was almost zero ($0.3 \pm 0.8\%$) most of nests were considered to be reconstructed by only progeny females. Notwithstanding this, except one nest which produced only males, all reconstructed nests produced females and males. Dissection of females taken from just reconstructed nests showed that 31.3% of females were inseminated and most of them had mature oocytes. Reconstruction rate of nests founded by foundress groups in spring was significantly higher than nests founded by single foundresses. This results consists with results obtained in June to July (Itô, 1993).

A large nest was abandoned in October and a new nest was established by absconding swarming. This nest was, although it was established at the final stage of *R. fasciata* colony cycle in Okinawa, produced 520 adults including far more than 100 females. These results suggest that in Okinawan *R. fasciata*, colony cycle is partially bivoltinic.

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COLONY DECLINE IN A SOCIAL WASP *BELONOGASTER PETIOLATA*: WHAT ARE ITS POSSIBLE CAUSES?

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The process of colony decline and dissolution in independent-founding polistine wasps has been attributed to two distinct events in the colony cycle. West-Eberhard's (1969) model of colony decline in *Polistes* holds that the process is a result of the declining dominance and cessation of oviposition by the queen. An alternative or additional explanation, developed by Jeanne (1972) for *Mischocyttarus*, is that decline is brought about by a critically reduced food supply to the colony at the end of the cycle, leading to starvation of brood and their cannibalization by hungry adults. Observations on colonies of *B. petiolata* in South Africa did not support West-Eberhard's (1969) hypothesis: firstly, brood decline could commence in the presence of a dominant, reproductively active queen; secondly, loss/removal of the queen did not lead immediately to cessation of nest growth and brood care, and therefore did not mark the termination of the colony cycle. Rather, brood decline appeared to be caused by a progressive decrease in the ability of a diminishing worker force to deliver enough food to the nest to adequately feed both the reproductive adults (gynes and males) and the larvae. Thus an increase in the ratio of gynes+males to workers, coupled with an adult priority over food reception from foragers, was probably the ultimate factor causing brood starvation and decline. This pattern closely fits Jeanne's (1972) model of colony decline, with the difference that brood abortion in *B. petiolata* may be related more to disposal of dead and decaying brood than to feeding hungry adults.

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COLONY LIFE CYCLE AND SEX RATIO OF THE ANT
PALTOTHYREUS TARSATUS IN IVORY COASTU. Braun¹, B. Hölldobler¹ and C. Peeters²¹ Theodor-Boveri-Institut, Lehrstuhl Verhaltensphysiologie und Soziobiologie der Universität, Am Hubland, D-97074 Würzburg, Germany² CNRS URA 667, Laboratoire d'Ethologie Expérimentale et Comparée, Université Paris Nord, F-93430 Villetaneuse, France

Field studies including the excavation of 29 colonies of *Paltothyreus tarsatus* (Ponerinae) were conducted in the years 1992 to 1994. Some of the excavated colonies were obviously young, with one mated queen and several hundred workers. They did not produce sexuals. The worker populations of mature colonies were considerably larger than previously assumed, and reached 3830 workers. All colonies were strictly monogynous. The nuptial flights of *P. tarsatus* were observed a few hours after the first heavy rainfalls at the end of the dry season (February-March). The synchronized departure of males occurred before that of queens; later in the day a large aggregation was located above an exceptionally tall tree, and copulating pairs were collected at the base of this tree. We conclude that mating behavior follows the male-calling syndrome, unlike the report of Villet et al. (1989). Colony foundation is semi-claustral. Queen cocoons were collected already at the end of April, which indicates that production of the next generation of gynes begins before the end of the current mating season. Indeed, young virgin queens were found in the nests in July, and thus they live in the colonies for about seven months. In contrast, the first male cocoons occurred in September, and adult males were not found before December/January. In the bigger colonies (>1000 workers), several hundreds of sexuals are produced (maximum was 1495 males in a colony of 3830 workers, and 769 gynes in another colony with 3081 workers). In the majority of nests sampled, males were more numerous than gynes. However, considering the considerable sexual dimorphism of gynes (dry weight of gynes is three to four times that of males, fat content is five times higher), the investment-sex ratio is female-biased.

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COMPARATIVE STUDY OF LIFE HISTORIES TRAITS IN SEVERAL SYMPATRIC MACROTERMITINAE SPECIES

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In a West Africa humid savanna (Lamto, Côte d'Ivoire), termite communities are dominated by four sympatric species of subterranean Macrotermitinae: *Ancistrotermes cavithorax*, *Pseudacanthotermes militaris*, *Microtermes toumodiensis* and *Odontotermes pauperans*. The mound-builder species, *Macrotermes bellicosus* is also present, but at very low densities. Ecological segregation is characterized at different stages of the colony life cycle. The founding stage is used to estimate post-settlement survival of reproductives, both in the laboratory on different soil substrates and in the field by experimental establishment of reproductive pairs. The ergonomic stage is studied to learn about the nest structure together with the spatial and temporal dynamics of fungus-comb chambers. Comparative foraging strategies are also observed, as well as food collection on different grass and tree baits. Feeding diet is studied both in the laboratory on young colonies and in the field for the most common species. The reproductive stage is used to observe species swarming strategies, mainly temporal segregation whose determinism is linked with climatic conditions. Spatial nest distribution of species is mapped in different macrohabitats along a toposequence (tree and grass savannas, gallery forest). Within each vegetation type, microhabitat utilization is determined at the scale of earthmounds colonized and modified by subterranean species. Niche breadth is then compared between the species. Different patterns for nest structure are shown between species in the vertical/horizontal distribution of fungus combs. Hypotheses are formulated about the possible reason for the dominance of the subterranean species and the scarcity of the mound building species. Life history traits are related to the importance of fungus-growing termites in organic matter recycling and ecosystem dynamics.

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SEASONAL VARIATIONS OF SUBORDINATES EGG-LAYING BEHAVIOUR IN THREE *POLISTES* SPECIES

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Egg-laying of subordinates in queen-right colonies was studied in three species of *Polistes* in Ukraine. Eggs were laid both by the co-foundresses and by the workers. The queen aggressively pursued and attacked such females trying to expel them from a nest. The dominant behaviour connected with the co-foundresses' oviposition in pre-emergence period was the strongest in *Polistes nimpha* colonies. Co-foundresses in *P. nimpha* were expelled by the queen in greater number of pleometric colonies observed than in *P. dominulus* ones. The egg-laying of workers was registered : in early post-emergence period - for pleometrotic *P. nimpha*, gaplometrotic *P. chinensis*; in later stages - for gaplometrotic *P. nimpha*, pleo- and gaplometrotic *P. dominulus*. Only *P. chinensis* workers guarded their eggs. The appearance of co-foundresses' and workers' ovipositions after some period of ritualized dominant behaviour changed rapidly queen's aggressiveness.

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VARIABILITY OF DENSITY OF BUMBLEBEES IN EUROPE

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Bumblebees are related to cooler regions of temperate climatic zone. This is confirmed mostly by many studies on species diversity of these insects, however, little is known on their number (density) in various latitudes. Recently, the author has carried out evaluations of bumblebees densities in natural ecosystems and on crops in various places of Europe: Poland, Rumania, Bulgaria, Germany, Belgium, southern France. Moreover, densities of bumblebees on red clover were earlier recognised by many writers for the whole territory of Poland. The results of studies suggest a clear relationships between bumblebees density and the value of coefficient of thermal continentalism (CTC) in Europe. Bumblebees density increases with a fall of CTC, i.e., with the increase in the effect of oceanic climate (hypothesis of oceanic-continental gradient of bumblebees density). In the northern and western part of Poland with CTC below 43% bumblebees density is considerably higher (over 2000 indiv./ha) than on the south-eastern areas (below 1000 indiv./ha) where the influence of continental climate is stronger. Similarly low values of bumblebees densities were also observed on lowlands of Rumania and Bulgaria where CTC value is close to 60%.

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GENETIC STRUCTURE OF SIX POPULATIONS OF THE ARGENTINE ANT *LINEPITHEMA HUMILE* (= *IRIDOMYRMEX HUMILIS*) AND THE MECHANISMS OF GENE DISPERSAL.

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The unicolonial Argentine ant *Linepithema humile* (= *Iridomyrmex humilis*) was long believed to be severely inbred, because alates mate inside the nest. However a first sample studied with allozymes techniques (Kaufmann *et al.*, 1992) did not show any inbreeding at the nest level. New samples collected in different locations produced similar but somewhat more variable results. We used the same enzymatic techniques to conduct this study, and of the six populations sampled only one (from Perth, Western Australia) had an inbreeding coefficient significantly different from zero. The five other populations showed no inbreeding, but gene flow appeared to be viscous in two populations (from La Grande-Motte and Antibes, both on the French Mediterranean coast). The main reason for the high inbreeding estimates in the Australian sample seems to be isolation between nests, located on trees growing on the regularly inundated shores of a lake. The water probably acts as a physical barrier, preventing the exchange of genes between the different nests. The two French populations where population viscosity was detected, are also the ones with the largest mean distance between the nests collected. Gene flow in the Argentine ant could thus be characterised by a sensitivity to natural obstacles or terrain features and maybe distance between nests. The mechanisms of gene spread in this species are mostly based on the absence of colonial barriers and the high rate of movement and exchange of individuals of all castes between nesting and foraging sites throughout the year. However, we have to take account of incest avoidance, male flight (Keller & Passera, 1993) and other such seemingly redundant features in that species. Those traits might have evolved because of the high frequency of "split budding" resulting in the invasion of a new site by a very few reproductive individuals and the loss of contact with the original population. Also the likelihood that in its native ecosystem the Argentine ant might be in competition with other ant species, resulting in a more patchy local distribution of nests, could make the flight of males necessary, at least when females are absent or late in coming.

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BIOGEOGRAPHICAL STUDY ON SYMBIOTIC FLAGELLATE FAUNAE OF TWO TERMITE GENERA *HODOTERMOPSIS* AND *RETICULITERMES* IN FAR EAST ASIA

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Symbiotic flagellates (Zoomastigophorea: Trichomonadida, Hypermastigida, Oxymonadida) which inhabit in the hindgut of termites have important role in cellulose digestion. Generally the species compositions of these flagellates are known to be host-species specific. However, detailed examination had not been made especially among nearly related host species. In this study flagellate species compositions of host colonies are investigated about two termite genera, *Hodotermopsis* (Termopsidae) and *Reticulitermes* (Rhinotermitidae) around the Japan Archipelago, and the similarities of compositions are studied. Colonies of *Hodotermopsis* spp. from Nansei Archipelago, Taiwan Is. and southern part of China have unique flagellate fauna, including *Eucomonympha*, *Hoplonympha* and many *Pyrsonympha* species. A morphologically interesting Trichomonad is also found out which have two akaryomastigont systems. All the colonies have basically identical flagellate composition. *Reticulitermes* colonies were examined about the region from Hokkaido Is., the northern end of the Japan Archipelago, to Taiwan Is. Five pseudergates per a colony were examined about presence or absence of each flagellate species. Results of cluster analyses on flagellate faunae shows difference of compositions corresponding to host species (or subspecies), suggesting phylogeny of hosts has a major effect on their symbiont compositions. All the colonies are more roughly divided into three clusters and the greatest boundary shows accordance to Watase line, a biogeographical border. This is thought to be the reflection of geo-history of the Japan Archipelago.

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APPLICATION OF A BIOGEOGRAPHIC MODEL TO EVALUATE THE
ANT DIVERSITY IN DIFFERENT UNITIES OF TERRITORY IN THE
SOUTH-AMERICAN TROPICS

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Studies made on large populations of a range of organisms, such as birds, have shown that the local specific diversity is a function of the territory surface where the community has been inventoried (Preston, 1962; Blondel, 1986). This function is a simple linear relation between the logarithms of both, area and number of species, if the samples belong to the same biogeographic region (Blondel, 1986). Using informations of a previous paper (Delabie *et al.*, 1993) and data taken in the ant collection of the Myrmecology Laboratory, we determine a similar relation for the ants of the State of Bahia ($\log S = 2.36 + 0.05 \log A$; $r^2 = 0.93$), using different territory unities in which the ants have been sampled, from 0.01 to 550,000 km². This function is compared with that determined from available published data for the State of São Paulo, situated 1500 km south from Bahia and where the local ant fauna is probably the best known for the Neotropics. We conclude that the number of ant species can be predicted for defined area of the same biogeographic region. Furthermore, an ant fauna showing strong differences of its richness/area ratio in comparison with the other observations, has to be considered isolated or belonging to another biogeographic region.

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LEARNING ABILITIES OF HONEYBEES AND PAPER WASPS

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In the field experiments bees (*Apis mellifera*) and wasps (*Paravespula vulgaris* or *P. germanica*) were found to be able to determine positions of a moving food source on the base of certain more or less abstract characters. In order to study if bees and wasps can differentiate "left" and "right" irrespectively to external cues they were trained to come into a nontransparent cylinder opened from above. A horizontal lath with two visually identical cups (feeders) was hanged at the internal wall. There was the sugar water in one cup and the natrium chloride solution in the other. The position of the lath was changed after each insect visit but rewarded cup remained constantly left or right in reference to direction from the center of the cylinder to the lath. In 13 out of 18 bees examined and in all 9 wasps statistical preferendum of the rewarded cup formed during some dozens of visits (the first choice was registered in every visit). Presence of mobile external marker (blue vertical stripe) near the end of the lath with rewarded cup did not facilitate the task although usually both characters of the reward were learned. Additional role of celestial cues could be supposed sometimes. Thus insects used three reference systems in parallel. In the other series of experiments there was a pair of rewarded and unrewarded cups at a small table. The pair as a whole was immobile while the positions of the cups alternated regularly after each insect visit. In the first variant where both cups were situated at the equal distances from the hive, most insects could learn the rhythm of alternation predicting position of the rewarded cup. In the second variant where the cups were situated along the direction to the hive insects preferred the nearest cup. But the learning occurred if the second experimental variant followed the first one. In the third and the most complicated variant four alternative positions of two cups were designed. After training during some days three bees out of 12 examined learned the regularity in this alternation. This task seems to be at the border of insect abilities.

WORKER OVIPOSITION AND KIN RECOGNITION OF THE STINGLESS BEE *SCAPTOTRIGONA* *BARROCOLORADENSIS*

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Workers of the stingless bee *Scaptotrigona barrocoloradensis* lay eggs even at queenright colonies. While colonies are rather small, they only lay trophic eggs at top margin of brood cells, and those are eaten by the queen before her oviposition. But in matured colonies, they sometimes lay a reproductive egg into the cell without queen's interruption or her oviposition. In such cases, the percentages of cells which receive a worker egg is up to 25%. They lay eggs only at an earlier period of age sequential task performance, and foragers don't produce eggs. When conspecific non-nestmate foragers were introduced into the small observed colonies (in which workers don't lay reproductive eggs), they were all rejected by guards. However, conspecific non-nestmate callows were accepted as often as were nestmate callows, although guards recognized difference. Acceptability of the callows was able to be modified with environmental odors derived from nurse bees or nest construction material including food stock. The capability of workers to discriminate nestmates which have different degrees of kinship can increase inclusive fitness, accepting only workers highly related in kinship, and maximizing the contribution of male production of the accepted workers. For example, in *Melipona fasciata*, the percentage of cells which receive male eggs produced by workers is 1%; and the guards of this species discriminate between nestmate callows and non-nestmate callows. While in *Trigona minangkabau*, a species in which worker oviposition has not been observed, the guards accept non-nestmate callows as often as nestmate callows. In *Scaptotrigona barrocoloradensis*, it should be anticipated that queens mate only once, or that the guards' kin recognition within a colony is variable depending on the colony size.

BEHAVIOUR OF YOUNG HONEYBEE WORKERS: AN EXTENDED PROCESS OF MATURATION?

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Young honeybee workers, up to 4 days of age, differ in their behaviour from older workers since they stay most of their time inside empty cells. In literature concerning 'division of labour' these young workers are usually classified as a distinct 'task group', dedicated to 'cell cleaning'. This paper addresses two main questions concerning the behaviour of young workers:

1 - Are there significant individual differences with respect to the amount of time of staying in empty cells among a group of equally aged workers? Such individual differences have been found for various other behavioural acts of workers inside the hive.

2 - To what extent do workers in cells actually move, and therefore possibly clean cells, or remain motionless ('rest')?

The occurrence of staying inside empty cells, as well as the movements the workers made inside cells was observed in three groups of 200 equally aged, individually marked, workers during the first five days of their lives.

The possible significance of the behaviour of young workers in terms of the 'division of labour' concept will be discussed.

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ON THE GIRDLING AND CANNIBALISM IN THE ORIENTAL HORNET, *VESPA ORIENTALIS* (HYMENOPTERA: VESPIDAE), IN THE OASIS OF THE SOUTH-WESTERN KIZIL-KUM

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The oriental hornet (*Vespa orientalis*) is widely distributed in semiarid environments of the Middle Asia. The natural aculeate hymenopteran fauna of Ayakgudzumdy oasis (Bukhara region, Kizil-Kum desert) was studied during six years. The oasis is not large (about 8 ha) and well isolated from other non-desert territories. There were no hornets occurred here in the first three years of our study. In the April of the next year a single hornet nest was found in a wall cavity. It seems that some hornet queens were introduced in previous autumn with an accidental car transported fruits from Bukhara oasis. In hot period hornet workers began to girdle almost all top twigs of *Eleagnus* trees of the oasis. Mass girdling of *Eleagnus* is probably done for sugary sap and less for fiber collection. It may be a result of a strong decreasing of nectar sources in summer. Girdling foragers formed groups on damaged twigs. Each previously marked forager came constantly to the same girdled area. If the girdle became too dry foragers often preferred the nearest fresh one. In October the large number of hornet males swarmed near single bastard acacia tree used as a terrestrial que of swarming. Hornet foragers have been occurred to catch and malaxate weakened males at swarming area. It may be a result of the absence of other large insects as a protein food in the oasis during deep autumn. In next years the hornet population in the oasis disappeared probably as a result of bad thermal conditions of the winter.

AREA MARKING IN THE ANT *PHEIDOLE PALLIDULA*

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By observing the tracks left by ants on smoked glass and by quantifying their orientation and their linear and angular speeds under different conditions, it was shown that, in *Pheidole pallidula*, the minor workers mark newly discovered areas by a discontinuous deposit of small amounts of their Dufour gland contents. The minor workers are stimulated to do so by major workers, which deposit, rather continuously, some quantity of their own, different, Dufour gland contents. This marking is not colony-specific. It is very rapid, thanks to the cooperation between the two kinds of workers, and it quickly vanishes in the course of time. This enables the species to rapidly colonize new areas and to keep them marked only as long as they are useful to the society (for example, during presence of food).

KLEPTOPARASITISM AND THE EVOLUTION OF SOLDIERS IN AUSTRALIAN GALL THRIPS

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Parasites and predators have long been considered to be one of the main ecological causes of the evolution of social behavior, but few studies have compared attack rates between social forms and their non-social relatives. If workers and soldiers evolved in the context of selection by invaders, then depending upon whether defense was highly or only occasionally effective, social forms might be expected to exhibit either lower or higher rates of successful invasion. However, a strong prediction can be made that eusocial forms should *not* have lower rates of attempted attack (whether successful or not) than related non-eusocial forms.

Koptothrips are kleptoparasites of Australian gall-forming thrips. These thrips, which are mainly host-specific, invade galls, kill their hosts, and breed inside. Rates of *Koptothrips* attack and invasion were consistently and substantially higher in five gall-forming species with soldiers (mean 24%) than in nine species without soldiers (mean 14%). I hypothesize that this difference has three causes: (1) a high proportion of *Koptothrips* invasions occurs before soldiers have eclosed, (2) *Koptothrips* are often successful in killing soldiers, and (3) if *Koptothrips* were not a common, persistent threat, then soldiers would never have evolved and been maintained.

These data on Australian gall thrips suggest that eusociality may sometimes represent an irreversible adaptation to stave off evolutionarily-persistent threats, rather than an "advanced" or "progressive" trait that leads to increased population size or decreased vulnerability to extinction.

BEHAVIORAL ATTRIBUTES AND PARENTAL CARE OF VARROA MITES PARASITIZING HONEYBEE BROOD

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Varroa jacobsoni an ectoparasite of the Asian honeybee *Apis cerana* has been introduced world-wide, and is currently decimating colonies of the European honeybee *Apis mellifera*. *Varroa*'s reproductive cycle is tuned to that of drone cells, those mainly parasitized in the original host. We describe here how a single fertilized female, infesting a brood cell, can produce 2 to 4 adult fertilized females within the limited time span of bee development (270 hr in worker and 330 hr in drone cells), despite the perturbations caused by cocoon spinning and subsequent morphological changes of the bee. From observations on transparent artificial cells we were able to show how the mite combats these exigencies with specialized behaviors used to avoid destruction by the developing bee, prepares a feeding site for the nymphs on the bee pupa, and constructs a faecal accumulation on the cell wall which serves as a rendezvous site for matings between its offspring. The proximity of the faecal accumulation to the feeding site facilitates feeding by the maturing progeny. However, communal use of the feeding site leads to competition between individuals, and protonymphs are most disadvantaged. The number of females produced per mother in multiinfested cells is reduced, but the probability of being mated is increased. This is due to the higher proportion of cells where at least one male reaches adulthood. Use of a common rendezvous and feeding site by two or more *Varroa* mothers in multiinfested cells can be considered to have developed from the parental care afforded to them as nymphs.

OBLIGATE MYRMECOPHILY IN THE ORIBATID MITE *ARIBATES JAVENSIS*

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We found the obligate myrmecophilous oribatid mite *Aribates javensis* Aoki et al. in the nests of a myrmicine ant *Myrmecina* sp. in West Java, Indonesia, as the first record of ant guest among oribatid mites[1]. The oribatid mite is quite peculiar in lacking sensilli, soft body, and the variable number of anogenital setae[2]. Colony of *Myrmecina* was composed of 10 ergatoid queens and 80 workers on average. All *Myrmecina* nests examined had a number of eggs, nymphs, and adults of *A. javensis* which were found only in nests of *Myrmecina* sp. The oribatid mites were unable to move by themselves. The ants took care of all stages of the oribatid mite in their nests and they helped oviposition of the mites. The mites can not survival without ant attendance. A few species of the genus *Myrmecina* specialize to some degree on oribatid mites as prey[3]. In the case of Indonesian *Myrmecina* sp., workers and larvae rarely fed on the symbiotic oribatid mites. However, dead mites were immediately consumed by adults and larvae. During severe food shortages, living mites were also frequently eaten by ants. Thus, the mites function as prey after their death or under starvation condition of ant colonies. However, the effects of the oribatid mites as prey on egg production and larval survival of the ant colonies were obscure.

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**ARMY ANT GUESTS AND ASSOCIATES: A NEW ANALYSIS
OF FUNCTIONAL RELATIONSHIPS**

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The symbiotic association of numerous arthropods and vertebrates with army ants makes of the army ant colony a complex community of diverse organisms with a level of biotic pluralism not achieved elsewhere among the ants. These symbionts and associates are so perplexing in variety of form and behavior that they have successfully defied attempts to categorize them in ways that clearly reveal their roles in the life of the army ant colony. The most enduring of these attempts is the system devised by Wasmann (1894), who considered in his analysis the nature of the symbiont/army ant interaction. Most recently Kistner (1979) rated symbionts as integrated or nonintegrated, depending on the degree to which they are integrated into the social organization of their host. I propose here a different approach that considers (1) the habitual or primary location of the symbiont or guest and (2) the major food source for the symbiont. It is logical first to sort species into intranidal symbionts and guests and extranidal symbionts and associates. Intranidal symbionts and guests include (1) facultative predators, (2) facultative and obligatory commensals, including phoretic species, (3) obligatory symbionts, both predators and prey-feeders, and (4) ectoparasites. Extranidal symbionts and associates are, with the exception of those species that live in the middens, "camp followers" that locate and follow army ant columns and swarms and usually attack flushed arthropods or the army ants themselves. They include (1) facultative detritivores and scavengers that live in the middens, (2) facultative predators of two types, those that prey on host ants and other arthropods that frequent the middens and those that locate army ant columns and attack the ants, and (3) swarm followers that attack potential army ant prey or steal prey directly from the worker ants and scatophagous butterflies that feed on the fecal/excretory droppings of swarm-following birds.

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FLUCTUATIONS OF THE CHEMICAL SIGNATURE OF TWO SPECIES OF PAPER WASPS (*POLISTES BIGLUMIS BIMACULATUS* AND *P. ATRIMANDIBULARIS*) DURING A CYCLE OF PARASITISM.

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Polistes biglumis bimaculatus may be parasitized by *Polistes atrimandibularis* during its 3-to 4-month colony cycle. In the present study, the chemical signatures of both species were analysed and determined using GC-MS, before, during, and after this cycle. These signatures are mixtures consisting mainly of cuticular hydrocarbons, which are used by insects for species recognition. The main difference between the two species, in a non-parasitic context was the fact that monounsaturated alkanes were present in *P. atrimandibularis* and not in *P. biglumis bimaculatus*. All the other substances were the same qualitatively, but their quantitative levels differed greatly. After one month of parasitism (end of June, beginning of July), when the two queens still had no descendants in the nest, the signature of *P. atrimandibularis* was an intermediate one. In July, when the female *P. atrimandibularis* was alone with a few females of *P. biglumis bimaculatus*, she acquired exactly the same chemical signature as the latter. In August, when there were males and females of each species with the queens, the signature of *P. atrimandibularis* was again intermediate, and in September, it tended towards the original pre-parasitic signature. The chemical signature of *P. atrimandibularis* therefore depends entirely on the social environment, whereas that of a colony of *P. biglumis bimaculatus* seems to simply evolve with time, regardless of whether or not it is parasitized.

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GENETIC DIVERSITY OF WORKERS AND INFECTION BY THE PARASITE *NOSEMA APIS* IN HONEY BEE COLONIES (*APIS MELLIFERA*)

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Multiple mating by queens of honey bee and other Hymenoptera has been much discussed. This is not only because polyandry represents an intriguing problem for the Kin-selection explanation of eusociality; it might also be an important cause of variation in female mortality. Hamilton (1987) and Sherman *et al.* (1988) independently presented a hypothesis that polyandry, while increasing workers' genetic diversity, also increases the probability of survival and reproduction colonies when they are invaded by a parasite or pathogen. Here we present the results of an experiment in which 10 honey bee colonies of high and low worker genetic diversities were infected with the wide-spread protozoan parasite *Nosema apis*. Sixty three days after infection, the number of the parasite's spores in the workers' intestines was estimated to investigate if there was greater variation in colonies with greater genetic diversity of workers. In all colonies there were two discrete groups of workers some containing few and others many parasite spores, therefore we calculated (1) the proportion of less-infected individuals, (2) the coefficient of variation for spore number in less-infected and strongly infected individuals. However none of the parameters yielded significant differences between the groups of colonies of different worker genetic diversity. This provides evidence not confirming the hypothesis tested.

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SOME PROPERTIES OF HOST-PARASITE INTERACTIONS
BETWEEN HONEY BEES FROM DIFFERENT GENERATIONS
AND THEIR MICROSPORIDIAL PARASITE, NOSEMA APIS

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Microsporidial parasite *Nosema apis* is a protozoon infecting usually honey bee, *Apis mellifera*, and sometimes also other Hymenoptera species. Such a narrow parasite specificity proves this host-parasite system to be a rather ancient one and reflects also partners phylogenetic properties, ancient phylogenetic systems having a tendency to decrease antagonism between system-forming partner species (Schuman, Dobrovolski, 1977). Such a decrease can be observed in honey bee families carrying always *N. apis*, the outbreaks of disease being, however, seasonal. In spring this parasite possessing no proper mitochondria and utilizing host energy sources is of great danger for bees survived after winter period, a lot of energy having been lost to assure optimal hive microclimate and to feed their spring brood.

Taking into consideration the full spectrum of parasite-host interactions - from "mutualism" during microsporidial proliferation up to antagonism during sporogeny and sporogenesis (Issi, 1986) - we tried to understand some factors responsible for Microsporidia pathogenesis in summer and winter honey bee generations. Temperature is thought to belong to the main abiotic factors influencing *Nosema* development. So we imitated summer temperature conditions (35-36 °C) and winter ones (20-22 °C) for winter bee generation in November-December in order to investigate their influence on *Nosema* life cycle. In 48 hours post infection (p.i.) at 20-22 °C meronts-1 were seen in middle and hind intestine together with a little quantity of "shooting" spores and sporoplasms. At 35-36 °C meronts-2 were observed together with meronts-1. Later the temperature factor had no influence on the duration of any stage of *Nosema* development. Up to the 7th day this parasite development was inhibited at meront-2 and sporont stages. Spores did not appear up to the 13th day p.i. at any temperature, infection having no effect on the frequency of bee death (7-10 % both in control and in infected insects). It is well known that parasite development is usually completed at the temperatures studied during 3-5 days p.i. in summer (June-July) honey bee generations; so we suppose the winter insects possess some yet unknown mechanisms blocking and "triggering" parasite spore formation. Investigation of these mechanisms is of great interest both for theory and practice of bee defense against nosematosis infection.

HONEY BEE HYGIENIC BEHAVIOR AND RESISTANCE TO VARROA MITES

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Hygienic behavior is considered the primary mechanism of resistance to at least two diseases of larval honey bees, and may be one mechanism of resistance to the parasitic mite, *Varroa jacobsoni* Oud. Resistance is conferred by hygienic bees detecting, uncapping, and removing diseased or infested brood from the nest. The removal response by honey bees to *Varroa* mites was previously noted only in *Apis cerana* and *Apis mellifera carnica*; however, hygienic behavior occurs in a low frequency in all races of *A. mellifera*. Hygienic and non-hygienic lines of *A. mellifera ligustica* ("Starline" stock) were selected using an assay which quantified the time required for bees to uncap and remove a comb section of freeze-killed pupae. The lines were then propagated through instrumental insemination. *Varroa* mites were introduced into cells containing pupae within specially designed comb fitted with removable cell bases (Jenter® Box). Within 24 hours, the hygienic colonies uncapped, and removed significantly more pupae from cells containing the introduced mites than did the non-hygienic colonies. In addition, hygienic bees opened and resealed cells containing *Varroa* mites, while no non-hygienic colonies were observed performing this behavior. The results indicate that it is possible to select among commercially available strains of honey bees for resistance to *Varroa* mites on the basis of hygienic behavior. Continuing studies will investigate the mechanisms involved in the detection of mite infested brood, and whether hygienic lines of bees are commercially profitable for beekeeping.

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EDIBLE HYMENOPTERA OF YUCATAN PENINSULA

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In the research line, Insects as source of proteins in the future, we record the edible insects of the Mexican Republic in order to know how insects contribute in the daily diet of people in the rural areas. In the Yucatán Peninsula we found 35 species of edible insects belonging to Hymenoptera Order, these are distributed among their families as follows in the Vespidae, subfamily Polistinae there are 13 species recorded, being the principal genus Mischocyttarus, Parachartegus, Polistes, Brachygastera and Polybia, in the subfamily Vespinae there is one species Vespula squamosa. In the Apidae family, subfamily Apinae, tribe Meliponini, there are 16 edible species and the principal genus are : Melipona, Scaptotrigona, Trigona and Nannotrigona also in the Apinae, tribe Apini are Apis mellifera ligustica and scutellata and in the Bombinae subfamily there is Bombus sp. Among the Formicidae we have recorded three edible species belonging to the Myrmecinae subfamily, Attini tribe, genus Atta and to the Dorylinae subfamily, Ecitonini tribe, genus Eciton. We can see that people exploit those insects qualified as Eusocial, among them, the stingless bees occupied the first place, eating not only the honey but also the brood, follow by the wasps with and without honey. We observe that this alimentary habit is very rooted among the peasants and comes from the prehispanic times prevailing yet today.

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THE POTENCIAL ANTIMALARIAN PROPERTY OF
MELIPONINAE PROPOLIS "IN VIVO"

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The mice life span after the malarian agent *Plasmodium chabaudi* inoculation depends on the number of parasites that had been injected. When inoculated with 10^4 merozoites, a 16 weeks old female BALB/c died around the 13th day. Similar groups of mice were treated with propolis from *Trigona spinipes* or from *Tetragonisca augustula* after infection with 10^4 parasites. These two last groups had presented a significant mortality alteration when compared with the first group (control). The handling consists in a daily injection of 20 μ l of 85% (w/v) propolis (ethanolic solution) during 10 days after infection. Every day, during the experiment span, it was made a circulation parasite count in all mices. They were individually marked. The final parasitaemic curves show a drastic reduction of this protozoa concentration in treated groups. When similar mice groups were treated during 10 days before infection we had no significant difference from the control infected group. These results suggest the reduction of parasite number depends on the toxic effect of propolis on circulating malarian parasites. Such propolis do not protect the mice but it kills the parasite. Other social insects products are beginning to be tested in order to carry out isolation and characterization of their active substances.

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LEAF-CUTTING ANTS (*Atta sexdens*) IMPACT ON NATURAL COMMUNITIES

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The leaf-cutting ants of the genus *Atta* (Hymenoptera: Formicidae: Myrmicinae) are thought to be important herbivores and modifying agents in natural communities throughout the Neotropical region (Fowler et al. 1989). We studied the leaf-cutting ant nests distribution in two 'cerrado' (Brazilian savanna) sites and concluded that their impact on natural ecosystems, although relevant, may be punctual and marginal on these areas. Furthermore, we believe that one of the most usual source of errors in the leaf-cutting ants impact estimates mirrors a bias imposed by some researchers at the fieldwork. In order to study the direct impact of the ants on 'cerrado' ecosystems, we determined some soil and plant structural characteristics both near the leaf-cutting ant nests and in paired areas without nests. Significant differences were found in the plant community, suggesting that the ants are really important as modifiers of local conditions. The tree densities in the nest areas are greater than without the influence of the ants, which, added to greater nutrient concentrations in their leaves, is a positive evidence to the Coutinho's (1984) hypothesis of nutrient local enrichment by leaf-cutting ants. Despite these findings, we hypothesize that the leaf-cutting ants impact on natural ecosystems such as cerrado is not as important as usually considered. This hypothesis is based upon their nest distribution, which was observed to be distinctly marginal in several cerrado ecosystems. The appraisal of the leaf-cutting ant nests density, as well as their penetration in the ecosystem, therefore, is very important in order to assess their impact on the natural ecosystems.

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INTRASPECIFIC COMPETITION THROUGH FOOD ROBBERY IN A HARVESTER ANT, *MESSOR ACICULATUS* AND ITS CONSEQUENCES ON COLONY SURVIVAL

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Intraspecific interference competition in a harvester ant, *Messor aciculatus*, was studied. Colonies do not have territories. Some nests were placed very close to each other, and the foraging areas of the neighbors mostly overlapped. Even though the frequency with which alien and owner ants met was very high in the vicinity of the nest entrances, aggressive interactions between them rarely occurred. However, when hostile workers encountered each other, they exhibited a kind of ritualized combat, and the winner ejected but did not injure it. If any aliens entered the nest, some of them were pulled out, mainly by the owners. Aliens roaming near the neighbor's nest entrance ferociously attacked the owners carrying seed in their mandibles and robbed them. On other occasions, the aliens entered the nest and stole the collected seed. Although seed robbing and stealing occurred among neighboring colonies, there were remarkable differences in the frequency of their occurrence. The results of field observations and experiments suggest the existence of a dominance hierarchy among the neighbors. One extermination of the inferior colony by its neighbor was observed. The raider colony stole only stored seeds from the nest of the inferior colony, and the larvae and workers were removed and deposited some distance away from the nest. The influence of ritualized combat and food robbing on colony activities, and the ecological significance of this interference behavior in terms of spatial distribution and temporal persistence of the nest sites, is discussed.

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THE INFLUENCE OF METEOROLOGICAL CONDITIONS ON THE FEEDING AND EGG LAYING OF THE QUEEN HONEY BEE, APIS MELLIFICA LIGUSTICA.

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It is well known by the beekeepers that the queen *Apis* lays more eggs when the weather is more warm. Now, the going and coming of the foragers were also dependent from weather. Is there a connection between these two factors? With the help of the workers marked (age known), we observed and counted the feeding behaviour and egg laying of the queen. The queen generally lays approximatively two or three eggs after having been fed once. The egg laying therefore is directly related to the rhythms of feeding. But the nurse bees of the queen are the young workers inside the nest. They do not go out and have no direct contact with the pollen gathering workers. They stay within the inner hive where the temperature is stable. In these meteorological conditions, we seize the opportunity of experiment during warm and clear weather as well as cool and cloudy weather. In that case, the behaviour of foragers and egg laying of the queen followed by the rhythm of the external temperature fluctuations. The registering of different physicals parameters inside the hive enable us to see the manner in which the nurse bees and the queen who do not go out, react to these meteorological conditions, thanks to the coming and going of the foragers which acts as indirect information.

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ROLES OF ACETATE AND OXYGEN IN METABOLISM IN THE PAUNCH OF THE HIGHER TERMITE *NASUTITERMES WALKERI*

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Nasutitermes walkeri is a higher termite living on sound wood. It secretes its own cellulase in the midgut and to a minor extent in the salivary glands; there is no cellulase activity in the hindgut. The absence of bacterial cellulase in the paunch makes it unlikely that glucose is the normal substrate for bacterial metabolism. A more likely candidate is pyruvate particularly as the lack of pyruvate dehydrogenase activity in the termite means that the termite is unable to metabolise pyruvate which is thus available for bacterial metabolism. Respiration studies show that glucose is metabolised at the overall rate of 16 nmol/termite/h which means that 32 nmol of pyruvate would be available for the bacteria. If this pyruvate is the only pyruvate used for energy production (and for gluconeogenesis), would its conversion to acetate generate sufficient energy for bacterial metabolism? A consideration of just one process, N_2 fixation, shows that this is unlikely. The rate of N_2 fixation in *N. walkeri* (0.45 nmol/termite/h) would require about 25% of the ATP produced. The problem is overcome if some of the acetate produced is oxidized via the TCA cycle and oxidative phosphorylation. Indeed, ATP for nitrogenase activity is normally produced by oxidative phosphorylation. The respiratory system of the termite allows direct access of gases into the hindgut and normal atmospheric gases such as CO_2 and N_2 as well as C_2H_2 are readily reduced so there is no reason why O_2 cannot also be reduced. A key question is how O_2 utilisation is balanced with the maintenance of the redox of the paunch (-230 to -270 mV).

Evidence will be presented to support the hypothesis that bacterial metabolism in the paunch of *N. walkeri* requires substantial reduction of O_2 .

PHYLOGENETIC RELATIONSHIPS OF THE GENERA OF NASUTITERMITINAE WITH MANDIBULATE SOLDIERS (ISOPTERA: TERMITIDAE)

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A group of 12 genera of exclusively neotropical termites is usually considered to represent the basal lineages in the subfamily Nasutitermitinae, with all degrees of intermediates between a fully mandibulate and a fully nasute soldier. A formal cladistic analysis of this group was conducted based on 34 morphological characters and two chemical characters. The nasute genera were pooled in a single terminal group since there is now good evidence that they are monophyletic. Characters were polarized using Apicotermitinae and Termitinae as outgroups. Exhaustive search using Hennig86 and equal weight for all characters produced 16 minimal length trees (CI= 67; RI= 76) and the following strict consensus tree: (*Procornitermes* (*Syntermes* *Cornitermes*) (*Labiatermes* *Paracornitermes*) (*Armitermes intermedius* (*Rhynchotermes* (*Embiratermes* *Ibitermes* (*Armitermes* *Macuxitermes* NASUTES (*Curvitermes* *Cyrilliotermes*)))))). Successive weighting resulted in six trees (CI= 83; RI= 88) and the following strict consensus tree: (((*Syntermes* *Cornitermes*) (*Labiatermes* *Paracornitermes*)) (*Procornitermes* (*Armitermes intermedius* (*Rhynchotermes* (*Embiratermes* *Ibitermes* (*Macuxitermes* (*Armitermes* NASUTES (*Curvitermes* *Cyrilliotermes*))))))). *Armitermes*, as presently defined including *A. intermedius*, is a polyphyletic group. *Embiratermes* is probably paraphyletic since it is defined by plesiomorphic characters and is not supported by any derived character. Contrary to the dominant view in traditional phylogenies, *Syntermes* does not appear as the most basal lineage, many of its putatively primitive characters being actually derived. Groups well supported include (*Syntermes* *Cornitermes*), (*Labiatermes* *Paracornitermes*), (*Curvitermes* *Cyrilliotermes*). The position of the nasutes is uncertain and making them the sister group of the mandibulate genera increases the tree length by only one step. Thus, the long frontal tube, the only character supporting the position of the nasutes among the mandibulate genera, may have evolved independently in both groups. Better resolution of the phylogeny of the Nasutitermitinae can be achieved by reconstructing the ancestral condition of the nasutes and of the outgroups.

ORIGIN AND DIVERSIFICATION OF THE *MICROSTIGMUS* WASPS (HYMENOPTERA, SPHECIDAE).

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Microstigmus is a highly interesting group within the Sphecidae, because of its nests and the social behavior exhibited by some of its species. The genus is exclusively Neotropical and closely related to the *alini* group within *Spilomena*, being distinct from it just by the loss of the Rs segment in the forewing (resulting in one submarginal cell). Both groups share a specialized denticulate area in the male 7th tergum. *Microstigmus* can be divided in six monophyletic lineages (characterized below by their synapomorphies). *Microstigmus xylicola*, *similis* and *alini* form the basal group which is characterized by having females with elongated head, integument with strong microsculpture, nests in wood burrows (made by beetles), and a bethylid as a parasitoid (Melo & Evans 1993). In the remaining groups within *Microstigmus*, the females have a vestigial spermatheca and a long, coiled spermathecal duct (functional spermatheca). *Microstigmus myersi* forms the next branch and possesses external nests built with soil particles (hanging from rootlets in banks) and long-haired larvae (Melo & Campos 1993). The sister group of *M. myersi* possesses a modified mesepisternum (presence of a transversal carina and a wide episternal sulcus). This group contains an unresolved tricotomy formed by *M. xanthosceles*, *M. puncticeps* and *M. (Trichostigmus) + M. (Microstigmus)*. *M. xanthosceles* has protuberant clypeus and a strong median keel in the first metasomal sternum (nest unknown). *M. puncticeps* has strong punctures in the frons and mesoscutum, and conspicuously hairy eyes (nest excavated in the substrate). The branch formed by *M. (Trichostigmus) + M. (Microstigmus)*, with nearly 80% of the species in the genus, contains the most derived forms and is characterized by petiolated external nests, adults with green eyes, pyramidal scutellum, males with yellow or white frons, and no cocoon spinning. *M. (Trichostigmus)* has a pair of long setae between the median and posterior ocelli. *M. (Microstigmus)* has a yellow integument, a wide malar space, pupae without head tubercles and Collembola as prey.

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SOCIAL DEVOLUTION IN SWEAT BEES

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Many genera and subgenera of Halictine bee contain both social and solitary species and at least seven species exhibit both solitary and social behaviour. Consequently, sweat bees in general and the socially polymorphic species in particular are prime candidates for the title "the holy grail of insect sociobiology". However, this statement rests on the assumption that solitary behaviour is ancestral and social behaviour derived in each case.

We have performed phylogenetic studies of the genus *Halictus* (Richards, 1994, *Insectes Sociaux*, in press) and the subgenus *Evyllaues* (Packer, 1991, *Behav. Ecol. Sociobiol.* 29:153-160; Taylor and Packer, in preparation) and Danforth and Eickwort have performed phylogenetic studies of the *Augochlorini* (in press). In each case, the socially polymorphic species appear to have had a eusocial ancestry. Similarly, in at least five genera/subgenera, the purely solitary species often represent a comparatively recent devolution from eusocial behaviour. In an additional case (*Halictus ligatus*) in which some populations are clearly eusocial and others have very weak caste differences (Packer, and Knerer, 1986, *Behav. Ecol. Sociobiol.* 18:363-375), it is the loss of marked caste differences that is the recent evolutionary change.

Thus, phylogenetic research indicates that it is far easier to document a recent evolution of solitary behaviour from eusocial ancestry, than it is to demonstrate a recent evolution of eusociality: reversals in social evolution would seem to be common in sweat bees. Why?

After documenting the phylogenetic patterns of social and solitary behaviour among the Halictidae some possible reasons for the ease with which these bees lose eusociality will be addressed.

PHYLOGENETIC RELATIONSHIP OF WASPS (VESPINAE) REVEALED BY RESTRICTION SITE ANALYSIS OF 28S RIBOSOMAL DNA

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The phylogenetic relationship of the german vespinae wasps, *Vespula vulgaris*, *Vespula rufa*, *Vespula germanica*, *Dolichovespula saxonica*, *Dolichovespula media*, *Dolichovespula sylvestris*, *Vespa crabro*, and the malayan wasp, *Provespa spec.*, was analysed by restriction site mapping of 28S rDNA. The analysed sequence is about 900 bp long, is located at the 5'-flanking region of the 28S rDNA and encloses two variable regions (D1, D2) as well as conserved intersperses. This sequence was amplified by PCR using two conserved primers. Several four-basepair restriction-enzymes were used singly and in combination to cut the PCR product and to construct restriction site maps. Three different nests per species were investigated to analyse intraspecific variability.

To support the restriction site maps and to demonstrate the suitability of the chosen 28S rDNA sequence for wasp phylogeny, this region was sequenced in *Vespa crabro*. Sequence comparison with solitary wasps, Drosophilidae and higher eucaryotes revealed that the investigated sequence is indeed an effective tool to analyse phylogenetic relationships between closely and distantly related species. Reason is, that this sequence is comprised of variable and conserved regions. No intraspecific variation between different nests was found. The restriction site comparison supports the monophyly of the genus *Dolichovespula* and the genus *Vespula*. The hornet (*Vespa crabro*), likely to be closest related to the common ancestor of Vespinae (Matsuura and Yamane, 1990), showed closer relationship to *Dolichovespula* than to *Vespula* species. *Provespa spec.* described as a 'link' between *Vespa* and the remaining Vespinae (*Vespa*+ (*Provespa*+ (*Dolichovespula*+*Vespula*)) (Carpenter, 1987) was shown to be closer related to *Dolichovespula* than to *Vespula* species.

The proposed monophyly of *Dolichovespula* and of *Vespula* is in accordance with results of an RFLP study of mitochondrial DNA (Schmitz and Moritz, 1990), as is the identification of *Vespa* to be closest related to *Dolichovespula*.

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THE ANTENNAL PATTERN OF SENSILLA OF *NOTHOMYRMECIA MACROPS* IN COMPARISON TO THOSE OF OTHER ANTS FROM THE MYRMECIINAE AND PONERINAE.

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The antennal pattern of Sensilla of the worker of *Nothomyrmecia macrops* CLARK has been studied with SEM. The results have been compared with those from SEM studies of 23 species of *Myrmecia* and other ants (WALTHER, 1984). Additionally, the antennal sensilla of the worker of *Myrmecia gulosa* have been studied with the TEM. Further studies of the antennal sensilla of numerous species from all other superfamilies of the Aculeata are under consideration (WALTHER, 1983). On the flagellae of *Nothomyrmecia* we can find with SEM 8 different types of sensilla. The poreless sensillum type x (WALTHER, 1981b) can only be studied by TEM. Three types belong to the olfactory sensilla (Sensilla trichoidea curvata, S. basiconica, S. trichoidea). Gustatory and mechanosensitive Sensilla chaetica, mechanosensitive tactile hairs and Sensilla campaniformia can be seen between the olfactory sensilla. The sense hairs of the Sensilla ampullacea are placed in a cuticular chamber about 40 µm under the surface of the antennal flagellae. In contrast, the sense hairs of the Sensilla coeloconica can be observed in the distal opening of the cuticular chamber. As one result of this study we must state that there are no remarkable differences between the pattern of Sensilla of *Nothomyrmecia macrops* and those of the 23 studied species of *Myrmecia*. We think that *Nothomyrmecia macrops* should be placed with all other species of *Myrmecia* in the subfamily Myrmeciinae. The results of this study do not permit to state that *Nothomyrmecia macrops* has a more primitive pattern of sensilla than the other 23 studied species of *Myrmecia*. In contrast, it seems to us more evident that *Nothomyrmecia*, which is a night active species, is slightly more evolved than *Myrmecia*. This assumption corresponds with other results from different wasp groups out of the Scolioidea. We cannot agree to the opinion of TAYLOR (1978) that *Nothomyrmecia macrops* is the most primitive living ant. From our own results of the comparative studies of the antennal sensilla we must state that we find ants with the most primitive patterns of sensilla in the Platythyreini (Ponerinae) (Walther, 1984).

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FACTORS INFLUENCING DOMINANCE RANKING IN THE FUNCTIONALLY MONOGYNOUS ANT *LEPTOTHORAX* SP. A

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Leptothorax sp. A is a functionally monogynous species, i.e. although many queens can be present, only one is reproducing. Queens can either be "gynomorphic" (winged) or "intermorphic" (wingless) and colonies may contain one of the two morphs or both of them. In addition to the finding that intermorphic queens establish dominance hierarchies with the onset of spring, we found another period in the colony cycle during which aggressive interactions occur. This is directly after the readoption of young queens into their mother-colony after mating. During both periods (fights after hibernation = period A; fights after adoption = period B), both queen-morphs were aggressive towards each other independent of the presence or absence of an old queen in the colony. Following period B, all queens (5.4 ± 1.6 ; $N = 7$ colonies) overwintered in the colony, but their number was reduced to 2.2 ± 0.9 after period A. The aggression of Alpha directed towards Beta-queens was significantly higher during period A than during period B, whereas the rate of aggression against Gamma-queens did not differ. As a result of the high aggression of Alpha against Beta, Beta and other subordinate queens ($N = 7$ colonies) emigrated from the colony in spring, probably to found their own colonies. The Alpha-position appeared to be very stable, e.g. one queen kept this position for three successive breeding cycles. The weight and thorax-length of 31 vs. 52 queens of both morphs was compared with the social rank these individuals acquired during dominance interactions. No positive correlation could be found ($r_s = -0.08$ vs. -0.09 ; ns). Age and fertility, two possible additional factors of influence to rank-acquisition are currently investigated.

COLONY CONTROL IN *POLISTES GALLICUS*: REACTIONS OF WORKERS TO AN ALIEN FOUNDRESS.

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In social wasps, a well developed kin recognition capacity prevents the workers to avoid helping any female parasites. In *Polistes gallicus* the intraspecific usurpation rate is about 7%. In a previous study, the ovarian development in workers which emerged after an alien foundress had taken the place of their mother, proved to be greater than in normal colonies. This fact has an obvious adaptive value. We hypothesized that the usurpers could deceive the host workers regarding their kinship by changing the odour of the nest. Conspecific usurpers, like social parasites, perform a certain behaviour (stroking) which is probably associated with the application of pheromones over the nest. The following experiment was aimed to determine whether the length of stay of the usurper on the nest prior to worker emergence, and the status of the immature brood at the moment of invasion, can influence the control an unrelated foundress has over the reproductive capacity of the workers. For this purpose, 32 foundresses were forced to accept alien conspecific nests in the pre-emergence stage: in 19 nests the most advanced stage of the brood were larvae (LN), whilst 13 nests contained pupae (PN). Sixteen control nests (CN), were reared under identical laboratory conditions with their own foundresses. No significant difference was found between the mean ovarian development in workers emerging from PNs ($X=15.7$) and LNs ($X=11.1$), however there were more potential egg layers in PNs than LNs. Moreover PN (but not LN) workers were more aggressive towards alien females than CN workers towards their mothers. Our results suggest that the longer usurpers stay on an alien nest before worker emergence, the more efficiently can they control the colony; they also agree with the hypothesis that usurpers can change the nest odour (Klahn, 1988) or in some way acquire it. However, it is possible that the presence of an alien foundress during the immature phase can also influence the behaviour and physiology of the workers. The variability in usurper colony control capacity could also indicate that an alien female needs some time to "familiarize" herself with the host nest.

OCELLAR FLIGHT CONTROL IN THE INDIAN GIANT HONEYBEE *APIS DORSATA*

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The giant Indian honeybee *Apis dorsata* forms some interesting problems for investigation of visual orientation especially due to its bigger size and mass. In the experiments, done in JNU, bees had been trained to fly to a feeder in the lab. Visual orienting behavior was video filmed in a flight chamber and assessed regarding various angular and kinetic parameters (e.g. the direction of the body's length axis, the flight course, the ground speed) under two motivations (*feeding* and *homing flight*) and two flight chamber regimes (*with side light on* and *without side light*), similarly as described in Kastberger and Schuhmann (1993) for *Apis mellifera*. Due to its higher mass, which is three times that of *Apis mellifera*, longer reactivity delays occur in the giant honeybee. Experimental occlusion of the ocelli will produce behavioral inconveniences which last longer and which are more striking than those in the smaller *Apis mellifera*. The findings lead to concepts for visual flight control which should be discussed with the special nature of this bee to fly in the dark (Dyer 1985; Kirchner and Dreller 1993) and to defend the nest by explosive attacks (Seeley 1987), that makes fast and distinct discrimination of objects and pretruders necessary, also in the dark. The ocellar system (a) stabilizes orientation control and makes it more invariant to ecological and motivational cues, (b) it promotes an arousal-dependent tool to sustain or improve positional adjustment, (c) it implements the capacity for the free-flying bee both to react faster and to fly more continuously. As the giant honey bee is known to be older than the European bee (Roubik 1989; Cornuet and Garnery 1991), differences in ocellar modulation of visual orientation determined between *A.dorsata* and *A.mellifera* might also inquire some evolutionary aspects in visual flight control.

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« LOST » BEHAVIOUR OF A HARVESTING ANT (*MESSOR WASMANNI*) IN GREECE.

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When an ant (*Cataglyphis bicolor* - Fab) is displaced to a place unknown she goes into a searching routine to find her nest, a series of circling paths. (Wehner & Srinivasan - 1981). We have examined this « Lost » behaviour of a harvesting ant (*Messor wasmanni* Krausse) searching for food from a trail, on the assumption that it might be different from that of an ant searching for a point, the nest, as compared to a line (the trail). We examined the « lost » response by plotting out paths of displaced ants in detail. They were like those of *Cataglyphis*, a circling procedure, the same for ants displaced from a trail as from activity round the nest entrance. Ants that had their eyes covered with opaque paint behaved much like normal ants. A computer model was made of an effective modified random searching procedure similar to that found but using no navigational information as available to *Cataglyphis* from the sky light.

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BEHAVIOUR OF SOME SOLITARY BEES IN SOUTH SINAI (A.R. EGYPT)

1. TERRITORIAL BEHAVIOUR OF ANTHOPHORA SP. NEV. (ANTHOPHORIDAE, HYM.).

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Male territory as well as energetics and water balance of the solitary bee, Anthophora sp. nov. have been studied in St. Catherine, South Sinai, in spring 1992. The male and female exhibit different activity periods, as the females are active early in the morning, collecting nectar and pollen, then their activity ceases at the mid-morning, while the males start foraging later in the morning feeding on nectar only. Females again are active in the afternoon once the males stop their activity. Male territoriality starting the morning synchronizes with the highest nectar production rates of the flowers (Alkanna orientalis) and usually extends till about 14 30 h. The territory area varies during the day and ranges from few to several meters in diameter, depending on the number of flower patches defended as well as the quantity and quality of rewards they contain. The male persists in the same territory for 3-8 days or more, feeding mainly on the flowers of the base patch(es) and his visitation rate is very high at the beginning of activity in the morning, while it is lower in the afternoon. Mating was observed only in the morning.

During territoriality the balance of energy budget fluctuates from day to day and the male bee does not suffer any water deficit.

COMMUNICATIONS AFFICHEES

POSTERS

THE CONSERVATION OF SOCIAL INSECTS: A JOINT INITIATIVE OF IUSSI AND IUCN

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Over the last years a shift in conservation has taken place from the conservation of species, to their habitats towards the management of the entire biosphere, including men himself.

After a successful period of social insects conservation in the seventies which led to the protection of red wood ants (*Formica* spp.) in Europe, little attention was payed to social insects from the conservation community. However, social insects are among the dominant animal taxa in the biosphere, and together with their social life style which includes permanent nest structures and overlapping generations, they represent a huge potential in modern conservation, the management of biodiversity. This makes the social insects prime candidates for monitoring biological diversity and environmental quality. Conservation of social insects is a joint issue of IUCN-SSC (The Species Survival Commission of the World Conservation Union) and IUSSI, which should result in a first step in the production of the following reports, covering a review of different aspects of social insects, the assessment of the threat and conservation guidelines.

1. Ants as hosts of butterflies
2. The European Wood Ants
3. Social parasites
4. Ants living in plants
5. Diversity of leaf litter ant fauna
6. Introduced ants and their threat to local faunas
7. Social insects and environmental change
8. Social insects and rehabilitation of degraded land

The final aim is to implement the use of social insects in global as well as in local conservation efforts, using the conservation network of IUCN.

Anybody interested in these issues, i.e. in contributing, preparing reports or commenting is asked to contact Donat Agosti, Chairman Social Insects Specialist Group, SSC/IUCN and Conservation Officer, IUSSI.

BEHAVIOUR OF YOUNG QUEENS OF MELIPONA BEECHEII BEFORE AND AFTER THEIR NUPTIAL FLIGHT.

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The behaviour of young queens was studied before and after their nuptial flight, in four small colonies of the stingless bee *Melipona beecheii*, without the presence of a laying physogastric queen, during the dry season in Costa Rica (Central America). Eight behavioural elements of the intensive social interactions with the workers were analyzed for each emerged queen after its acceptance in the colony. The behaviours "pushing" and "tapping" were observed for the first time in gynes of stingless bees and are described here. "Pushing" was found to be age-related (ANOVA, $p < 0.01$), and possibly plays an important role in the process of acceptance and integration of the young queen in the colony.

After the emergence of a young queen a phase of acceptance and integration in the colony can be distinguished, followed by a nuptial flight and a pre-oviposition phase, with an average total duration of 13 days.

Tanatosis (death simulation) was found to be practised frequently by young queens during the acceptance phase to escape from worker aggression.

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EFFECT OF MACERATION ON THE SUSCEPTIBILITY OF CERTAIN WOOD SPECIES TO TERMITES.

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Effect of maceration of thirteen wood species with irrigating and draining water in their level of resistance to *Amitermes destrorum* Desneux has been evaluated under laboratory and field conditions. Biological analysis was done to determine the species composition of microorganisms in each source of water. Irrigating water with its low diversity of microorganisms, did not change significantly the suitability of the tested timber species to termites. Maceration in draining water with its high diversity of microorganisms reduced significantly the rate of consumption on six wood species. The wood species which became less suitable for termites after maceration in draining water for 4 weeks were: olive, peach, sidder, sweet acacia, persian liac and indian almond. Change in suitability of some wood species after maceration in draining water may be attributed to the production of repellent or toxic metabolites and the hydrolysis due to the hydrolytic materials associated with wood itself.

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SEASONAL BROODDYNAMICS AND FOOD STORAGE IN MELIPONA BEECHEII (APIDAE: MELIPONINAE).

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Food storage and brooddynamics were followed for three years from December 1990 of in ten colonies of *Melipona beecheii* in Costa Rica. Monthly inventories were made of pollen and honey storage and brood production. It was found that brood production was highest in November-January, with on the average 2087 (S.D.=351) cells of which between 35-70% was young brood. Honey storage was largest in March-April, followed by a short period of pollen storage in May-June, when brood production was significantly lower, on the average 1253 (S.D.=241) cells.

These results indicate that colonies of *Melipona* invest in brood production during the last months of the rainy season (November and December) when foraging conditions are still poor. When abundant florecence starts in March, a large worker force is available to forage for honey and pollen as a reserve for the rainy season which starts in May and is characterized by floral scarcity. Even though floral conditions are still good in April-May, brood production already diminishes, which may be explained as an adaptive strategy in relation to the onset of the rainy season.

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PRELIMINARY SURVEY OF EAST AFRICA URBAN TERMITES

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The taxonomy and distribution of East African urban termites aren't fully known, particularly those of the Ethiopian area. Considering they cause many damages, in order to make a plan of research concerning possible forms of control it is necessary to know which species are present, their food habits, their relations with the termites living in the soil surrounding the buildings and the conditions of temperature and humidity to which they can adapt. This survey aims at answering the first question. The list of termites damaging human residence in Somalia and in Kenia includes 12 species but it is not definitive. At the stage of the research it seems that the more common urban termites in both countries are members of the *Termitidae* family, although not necessarily the same species. Two species of *Rhinotermitidae* are found in Kenia and in Somalia where only one of *Kalotermitidae* families is found. The latter, found on the outskirts of Mogadiscio, is the *Cryptotermes*, a species known as cosmopolitan. It shows a certain resistance to the drought, which is the first requisite to adapt to the drywood and to the scanty humidity of the buildings. The presence of the species *C. dudleyi* was recorded in Kenia also (Edwards - Mills, 1986). Among the termites collected in Somalia the genus *Odontotermes* is the most common. Not all species present in the area are capable of adapting to the urban ecosystem.

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LIQUID POLLEN SUBSTITUTES FOR HONEYBEES

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In a confined and pollen-insufficient condition such as greenhouses, a liquid diet may support honeybee colonies (*Apis mellifera*). Experimental diets consisted of 50 % sucrose solution (served as control) and varying percentage of yeast extract or other protein sources were examined. The liquid diet with 2 % protein gave the most favorable results in uptake, egg laying, and sealed brood production. When yeast extract (YE) was used as the protein source, similar uptake to control was observed if the concentration was less than 4 %. Higher concentration resulted in low uptake and high mortality in a small wire-cage (5 x 5 x 8 cm) experiment. When these liquid diets were fed at top bars in a colony, the amount of uptake parallels with amount of hoarding. In flight cages (2 x 2 x 2 m), 13 - 21 % more eggs than control were laid with liquid protein diets (2 % YE or polypeptone). In strawberry greenhouses the 2 % YE diet sustained larval development and egg laying of the queen, whereas the control sugar solution raised larval cannibalism in short time and decreased egg laying thereafter.

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OLFACTORY MIXTURE RECOGNITION IN THE HONEYBEE: COMPARED STUDIES ON RESTRAINED AND FREE FLYING BEES

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The foraging behaviour of honeybees comprises far range orientation and individual associative learning processes. It is known that mainly olfactory signals cue such behaviour. As floral odours are complex mixtures, we aimed to characterise the behavioral mechanisms underlying the recognition of such olfactory signals. For this purpose we underwent (i) a study of the olfactory discrimination abilities at the individual level using the conditioned proboscis extension (CPE) assay, (ii) observations of olfactory cued choices of free flying foragers in a bee flight-room (BFR). In both assays a mixture of nine components, known to be oilseed rape floral volatiles, was used as the conditioning stimulus (CS) and the individual components were then tested either separately (CPE) or in a choice situation versus the CS (BFR). In the CPE assay, after three conditioning trials (antennae contact with a sugar solution as the unconditioned stimulus associated to the CS, and food uptake as the reward), the percentage of individuals ($n = 30$) responding to the testing components showed that four components elicited high level of CPE (above 70 %) whether the others induced lower level of responses (20-50 %). In the BFR assay, bees were conditioned to visit an artificial flower device diffusing the CS associated with a food source. They were then tested in a choice situation between flowers diffusing the CS or one of the nine individual components. From the recording of the number of landings on the different scented flowers, it was shown that three components were not discriminated from the CS, whether the others were significantly less attractive than the CS. Among the components recognised at the same level as the CS, two were common to those eliciting high level of CPE. The data obtained in the two types of experiments convergently showed qualitative hierarchy among the components, with only some of them being salient cues in the conditioning mixture recognition. The occurrence of two common components being salient at both individual and population levels is consistent with the "priority cue hypothesis" (Getz and Breed, 1993), according to which a blend is perceived as similar to dominant components in terms of salience. Moreover this validates the use of the CPE assay to screen out such salient components with a predictive value for cues eliciting odour recognition in free flying bees.

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BREEDING BETTER BUMBLE BEES - A FRAMEWORK FOR RESEARCH ON BIOLOGY OF BOMBUS TERRESTRIS

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The bumble bee, *Bombus terrestris*, is being used as pollinator of various crops in greenhouses in the Netherlands. After its introduction in 1985 for use in greenhouse tomato, the demand for bumble bee colonies has grown continuously. Since the late 1980's bumble bee colonies are commercially available. The success of artificial rearing of bumble bees is unpredictable due to lack of knowledge of the biology of *B. terrestris*. Because the breeding of bumble bees is very labour-intensive, this unpredictability leads to higher costs.

The aim of our research is to increase understanding of the biology of *B. terrestris*, in order to optimize artificial breedings. In this respect two aspects of the life-cycle of bumble bees have to be considered.

The first aspect is colony development. Since bumble bees are univoltine, one single fertilized queen starts a new colony after hibernation. She rears the first batch of brood. When the workers emerge they take over foraging activities of the queen. From this moment onwards the queen solely lays eggs. When the worker force has reached a certain value, the queen switches from the production of workers to the production of reproductives (males and queens). We ask the following questions: What life history traits determine colony development? In what way or ways can a queen maximize her fitness in terms of number of reproductives?

Producing just as many reproductives as possible is not enough. Since bumble bees are annual, young queens must be able to survive the winter months. This leads to the second aspect of the life-cycle: the hibernation of young queens. We are interested in factors that induce hibernation in young queens. Our hypothesis is that hibernation (diapause) is obligatory in bumble bees and that queens can be selected for non-diapause. The incidence of non-diapausing queens might depend on their geographic origin.

THE LOCALIZATION OF FERRITIN IN THE COCKROACH *LEUCOPHEA MADERÆ* (BLATTODEA)

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The ferritin has been found in ER and secretory pathway of nine families from six orders and in the haemolymph of two species of Lepidoptera. The role of this protein is not yet clear, even if it has been demonstrated that the ferritin keeps iron's concentration at high level in solutions, in a non toxic form and quickly available. The ferritin could activates the transport of iron from the intestinal cells, where it is carried together with the food, to different tissues for molecular synthesis. Probably ferritin also has a protective function, as iron excess causes damage to the cells increasing the numbers of hydroxyl radicals. We have identified the ferritin in the haemolymph of nymphs and adults of *L. maderæ* by electrophoretic methods. Our results show that the protein is stable to heat (75°C) or in presence of SDS. Gels were stained for iron with Ferene S by the method of Chung and then for protein with Coomassie brilliant blue R.250. The native form has an Mr. of about 450,000. It was eletroluited and then denatured, the polypeptides were separated by SDS-PAGE. The ferritine has three subunits with relative Mrs of 88,000, 66,000 and 60,000.

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Worker interactions and orphaning in *Cataglyphis cursor* (Hymenoptera, Formicidae)

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The interaction movement pattern among nestmate individuals and interindividual distances were analyzed in queenright and queenless *Cataglyphis cursor* societies. Experiments were carried out in a cylindrical box, divided in eight equal parts, devoid of familiar cues. Data were recorded for 15 minutes using a computerized moving image analysis. The number of isolated or contiguous empty sections, the worker arrangements, alone workers, workers in twos, threes, fours, etc..., measured interindividual distances. Frequency and duration of arrangements gave an account of the behavioural changes. Two situations, with 8 colonies, were considered : 1° Groups of ten workers, queenright workers with the queen (12 tests), queenright workers without the queen (12 tests), queenless workers without the queen (12 tests), were observed. 2° The second situation was the replication of the first one with addition of a marked intrusive worker taken from an alien society. The results confirm the present queen influence and attraction upon workers (first situation). The rate of change in worker number at any point in time is weaker than in the missing queen groups. In general, queenless groups do not behave in a different way from queenright missing queen groups. As a consequence of unfamiliar worker intrusion (second situation), worker interaction varies according to the environmental factor (presence of the queen in the society). Both types of queenright groups change through increasing activity, more alone workers, more arrangements in twos, threes, fours, fives, than in queenless groups. Queenless groups usually fail to adopt an economic and efficient strategy. Experimental evidence of the effects of orphaning influencing group efficiency and cohesion is reported. The results may have a significant meaning for consequence of interindividual communication and partly explain absence of natural queenless societies in spite of effective thelytokous parthenogenesis in *Cataglyphis cursor*.

SEX LINKAGE ANALYSES OF THE HONEYBEE *APIS MELLIFERA* BY MULTILOCUS DNA FINGERPRINTING

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In the honeybee, as in most insects of the order Hymenoptera, sex determination occurs by a multiallelic single locus. The hemizygotes (carrying only one allele) or homozygotes develop to males whereas heterozygotes develop to females (Cook, 1993; Whiting 1943; Woyke, 1963).

Here we describe a method for determining sex linkage by multilocus DNA fingerprinting. The full set of multiple allelic marker revealed by DNA fingerprinting is a powerful tool of screening the genome for linkage analyses. The test samples were taken from a queen instrumentally inseminated with one of her own sons ("self fertilisation"), which produced 50% diploid drones (homozygote at X locus) in one generation. Diploid drones from these colonies were reared in vitro with royal jelly (Woyke, 1963). The screening of sex linkage was performed using a DNA pool of 16 diploid drones and 20 worker bees. Each pool was digested with 4 different restriction enzymes and hybridized with 12 oligonucleotide fingerprint probes (Moritz et al., 1991).

The two DNA pools revealed the same allelic fingerprint marker composition except for those markers being closely linked with the X locus. The additional band in the worker bee pool represents the heterozygous sex allele linkage group. Counting the recombination events in single worker bees, the marker of the sex locus can be mapped.

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TOXICITY OF *Ricinus communis* EXTRACTS TO THE LEAF CUTTING ANTS.

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With the aim of determining the toxicity of plants on leaf-cutting ants, the effect of leaf organic extracts of *Ricinus communis* on *Atta sexdens rubropilosa* workers isolated from its nest and fed with artificial liquid diet were analysed. The crude extracts were obtained by the sequential method with solvents of increasing polarities (hexane, dichloromethane, methanol and water). To study the toxicity by contact, concentrations of 20, 100 and 200 mg/ml were used and each ant received the extract on the pronote, through a microsyringe connected with a micrometer. Extracts were previously incorporated to the liquid diet in the ingestion treatment, with 0.2; 1 and 2 mg/ml. The ants were distributed in lots of 60 workers to each concentration, which were put on Petri dishes (6 ants/dish) and maintained at the temperature of 25[±] 1°C and humidity of 60 to 80%. Mortality observations were made in a period of 24 hours, during 25 days. Statistic at analysis showed toxic action in extracts crude dichloromethane (contact) and methanol (contact and ingestion). These extracts were submitted to chromatographic column with silica gel as a stationary phase being obtained the following fractions: hexane, dichloromethane, ethyl acetate and methanol. It was observed that the methanol fraction of the crude leaf extracts presented greater toxicity. Thus, *Ricinus communis* leaves contain toxic chemical substances to *Atta sexdens rubropilosa* workers. These chemical have been studied in groups of polar compounds, such as terpenoids, alkaloids, polyalcohols and so on, which have been reported to show toxic activities to the ants.

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ANALYSIS OF THE ACTION OF THE PYRIPROXYFEN, A JUVENILE HORMONE ANALOGUE, ON *APIS MELLIFERA*.

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Pyriproxyfen, an analogue of the juvenile hormone of insects, when applied topically to larvae and pupae of africanized *Apis mellifera* workers causes alterations demonstrated by the change in pigmentation pattern, especially in the eyes and thorax. This effect, which is provoked by doses of 1 μg , may prevent emergence, leading to insect death. Pyriproxyfen not only alters larval and pupal pigmentation, but induces vitellogenin (Vg) synthesis in adult workers confined for 7 days after emergence. However, treatment of these adult workers with pyriproxyfen only results in the partial induction of Vg synthesis. Thus other factors acting *in vivo*, such as quality of the diet and social interactions, appear to be involved (Bitondi and Simões, 1994), hampering the analysis of the action of this hormone on Vg synthesis *in vivo*. Incubation of the fat body with [^{35}S] methionine in culture medium and measurement of the incorporation of this amino acid into Vg and into other proteins respectively isolated by immunoprecipitation and acid precipitation have permitted the study of the possible direct action of pyriproxyfen on fat body cells. Measurements by liquid scintillation spectrophotometry and SDS-PAGE followed by fluorography have permitted the quantification and qualitative study of the proteins synthesized in the presence and absence of pyriproxyfen. We noted that 2.5 and 5 μg of this analogue (per ml culture medium used to incubate the fat bodies of 2 workers) do not affect total protein or Vg synthesis by the fat bodies of 7-day workers. The 5 μg dose also does not alter protein synthesis in the fat body of 0-day workers, who have a distinct synthesis pattern mainly characterized by small amounts of Vg. Higher doses (10 and 20 μg) cause a partial progressive inhibition of total protein synthesis both in 7 and 0 day-workers. Thus, there is no induction of Vg or other protein synthesis (detectable by SDS-PAGE and fluorography) in the fat body of 0 and 7-day workers in the presence of pyriproxyfen. The inducing action of this analogue on Vg synthesis observed *in vivo* must be associated with other factors and not with a direct action on fat body cells, as demonstrated in our *in vivo* and *in vitro* studies.

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ABUNDANCE, DRY WEIGHT AND TOTAL BIOMASS OF MICROTERMES FUNGUS COMBS (ISOPTERA; TERMITIDAE; MACROTERMITINAE) IN WOODLAND AND MAIZE CULTIVATED SITES AT MOKWA, NIGERIA

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Mean abundance (no./m²), mean dry weight (g) and mean total biomass (g/m²) of Microtermes fungus combs were examined to a soil depth of 1 m and, at 25 cm intervals to 1 m, in undisturbed primary woodland, 15 year old secondary woodland and newly cultivated maize over a three year period in wet and dry seasons. Abundance was higher in maize and secondary woodland than in primary woodland. Dry weights in the wet season were higher in primary woodland and maize than secondary woodland. Biomass was greatest in maize then secondary woodland. In primary woodland, abundance, dry weight and biomass did not differ between the seasons. Abundance was greatest below 75 cm in both wet and dry seasons with few combs above 50 cm. Dry weights were highest in the top 25 cm of the soil in the wet season and below 75 cm in the dry season. Biomass was concentrated below 50 cm and declined with decreasing depth. In secondary woodland, abundance was greater in the dry season than in the wet and declined with increasing depth. Dry weights were lower in the wet season than in the dry season. Biomass was greater in the dry season than in the wet season where biomass was greatest above 25 cm and declined with increasing depth. Wet season biomass was lowest between 0 and 25 cm and similar at all depth intervals below 25 cm. In maize, abundance was greater in the wet season than in the dry season with the greatest seasonal difference shown in the top 25 cm. Dry weights were similar at all depths below 25 cm in both seasons. In the top 25 cm, wet season combs were heavier and dry season combs lighter than at other depths. Biomass was lower in the dry season than in the wet season with wet season biomass greater than dry season biomass at all depths above 75 cm, especially between 0 and 25 cm.

TERMITE ASSOCIATIONS WITH VEGETATION PATTERNS IN ZIMBABWE.

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Studies in Botswana and Niger established that termites have an important role in the production and maintenance of land microvariability. Land microvariability is small-scale variations in soil properties and topography which are often reflected in vegetation characteristics. This study examined to what extent termites are associated with land-microvariability in SW Zimbabwe (38% of total country area). Land microvariability patterns were identified from air photograph interpretations and field investigations were carried out. Results show that termite nest building is associated with all but one type of land micro-variability, affecting over 13% of the land area in this region. Nest building (mounds) of two termite genera, Odontotermes and Macrotermes, are regularly associated with differences in vegetation composition and growth.

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CLASS III GLANDS OF THE VI ABDOMINAL STERNITE ARE INVOLVED IN PARASITIC RELATIONSHIPS BETWEEN IN *Polistes sulcifer* AND ITS HOST *P. dominulus*.

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"Stroking" is a remarkable behaviour exhibited by foundress females of *Polistes* throughout the whole colonial cycle and females of parasitic species soon after nest conquest. As stroking consists of rubbing the last gastral sternites on/inside the nest cells, it has been suggested that such behaviour allows any secretory product from glands in the terminal abdominal sternites to be smeared over the substrates. This research aims to ascertain whether the biosynthetic steps of the VI abdominal sternite glands in *P. sulcifer* and its host *P. dominulus* fit the different intensities of their distinctive stroking activity evaluated in the laboratory. Ultrastructural observations were performed under the scanning (SEM) and transmission (TEM) electron microscopes, using current methods. Preliminary SEM investigations disclosed that, besides the well-known glands which form a band just behind the antecostal sternal margin, both species also possess a further class III gland population, localized in the caudal half of the sternite. TEM analysis of the anterior glands showed a chain of functional steps common to the two species: a) inactivity, b) onset of biosynthesis activity, c) prolongation of activity, d) regression of biosynthetic apparatus, e) degradation of organelles. Comparing the gland- and life-cycle in *P. sulcifer* reveals that: 1) the day of usurpation (when the stroking intensity is at its max level) is marked by the onset of the secretory activity; 2) although the stroking behaviour falls abruptly three days after nest conquest, secretory activity continues for several weeks. A similar comparison in *P. dominulus* discloses that: 1) the secretory activity starts and continues during the pre-emergence (larval and pupal) period, when stroking activity is most intense; 2) during the post-emergence phase, the biosynthesis apparatus shows patterns of degradation, while stroking activity falls only slightly. Our observations reveal that stroking activity coincides only in part with the gland cycle, i. e. in its early phases. For a more complete picture, the results suggest to extend TEM investigation to the second (caudal) gland population.

COULD MONOAROMATIC COMPOUNDS BE A SOURCE OF ENERGY FOR SYMBIOTIC GUT MICROFLORA OF HIGHER TERMITE WITH DIFFERENT FEEDING GUILD ?

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In tropical and subtropical regions, termites with their important biomass play an important role in the degradation of organic matter. Their impact on the carbon cycle is mainly due to a diversification of their diet (i.e. wood feeding, fungus growing and soil feeding termites) which allow them to thrive on the majority of plant resource. Their digestive ability is link to a symbiotic relationship with their gut microbiota. Recent investigators have shown by feeding experiment that beside cellulose and hemicellulose, lignin contents or aromatic compounds could be totally or partially degraded by termites. However it is still unclear if this degradation (i) is share by all termite feeding guild (ii) is mediated by their hindgut microflora (iii) occurs with or without oxygen . In order to approach theses problems, a numeration of the aerobic and anaerobic gut microflora has been undertaken on two representatives lignin monomers ; syringic and ferrulic acid. This numeration has been done on Termitidae species as they represent in tropical area the most ecologically important family. Seven species, representatives of their respective feeding guild were assay.

The results of this study clearly show that :

- Within all the termite tested, the two aromatic compounds were degraded but at different extend in aerobic and anaerobic condition.
 - In aerobic condition, no significant difference in bacterial density (except for *Microcerotermes parvus*) were demonstrated between the different feeding guilds. This was not the case in anaerobic conditions
 - in anaerobic condition, only modification of the side groups occurred (no ring cleavage) except for the soil feeding termites where a degradation of the syringic acid in acetate was measured (up to 10⁵ bact/ ml of gut Eq).
 - In all termites and conditions (aerobic and anaerobic), the number of bacteria utilising ferrulic acid as a growth substrate were higher than on syringic acid suggesting that phenylpropenoids could be a better energy source that benzoic derivatives for the symbiotic microflora.
 - The Grass feeder (*Trinervitermes rhodosiensis*) and the fungus growing termites (*Macrotermes mülleri* and *Pseudacanthotermes spiniger*) possess, over the species tested, the highest bacterial density microflora on these two substrates.
- Some bacteria isolated from the last dilution tubes are currently identified. These results suggest that aromatic compounds could represent a food supply within the different feeding guild. Moreover, soil feeding termites seems to possess an typical anaerobic microflora which could degrades some aromatic compounds to acetate which can be further oxidised by the termite

ECOLOGY OF *LASIUS FLAVUS* MOUNDS IN LIMESTONE GRASSLAND IN IRELAND: SPATIAL DISTRIBUTION, SOIL MODIFICATION AND NEST VEGETATION

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Although *Lasius flavus* is still widespread and common throughout Ireland, areas where this ant achieves high densities of mound nests are increasingly rare due to agricultural activity. The observations reported here were made at 8 sites in mid-western Ireland where high densities of mound nests occur in shallow soils over limestone. Nearest neighbour analysis showed the nests to be spatially overdispersed and this is further supported by a Dirichlet tessellation analysis (Byers, 1992). A chemical comparison was made between soil taken from the top 10cm of mound and 0.5 metres from the mound. Levels of calcium, potassium, magnesium and possibly manganese were significantly higher in the mound soil, compared to the nearby soil. Mound soil conductivity was significantly higher, but it had a significantly lower pH. Multivariate analyses (PCA and discriminant function) were used satisfactorily to distinguish mound soil and nearby soil. Vegetation was studied by placing 5 quadrats (total area 0.25m²) on each of 12 mounds at 8 sites, plus 1 quadrat (area 0.25m²) 0.5 metres away (total 576 quadrats). A total of 102 plant species were recorded which represents a rich and diverse vegetation. Some plants were only found on the nests and others only off the nests. A few plants showed preferences for specific aspects or locations on the mounds. In addition, amongst the aculeate Hymenoptera, *Bombus distinguendus* Morawitz and *B. sylvarum* (L.), two bumblebees with a very restricted distribution in Ireland, and two uncommon ants, *Lasius mixtus* (Nylander) and *Myrmica schencki* Emery were recorded from one of the study sites. We conclude that areas where high densities of *Lasius flavus* mound nests occur are of high scientific interest and indicate sites which merit conservation.

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FORAGING BEHAVIOUR AND COLONY INTERACTIONS OF THE ANT *MESSOR ANDREI* IN CENTRAL CALIFORNIA**M.J.F. Brown**

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Eighteen colonies of the seed-harvesting ant *Messor andrei* were observed during the summer of 1993 in a serpentine grassland community in northern California. Colonies foraged along 2 to 7 directions (mean = 4.8). Each colony used from 1 to 6 foraging directions per day (mean = 2.06). A colony foraged in a given direction from 1 to 5 consecutive days (mean = 1.86). Foraging directions do not rotate as was suggested by Hobbs (1985). Foraging areas of colonies overlapped and were irregular in shape. Each colony interacted with 0 to 6 other colonies (mean = 2.06) over the summer, and with 0 to 3 other colonies on a given day. Interaction rates are related to local density, but not to nearest-neighbour distances. Experimental work shows that whilst colonies normally forage away from neighbours, the addition of seed bait results in foraging towards neighbours. Four of the 18 colonies relocated their nests during the study period. The behaviour of new queens was observed. Newly mated queens were observed to enter already established nests (Creighton, 1953). One newly mated queen dug a separate hole and was observed foraging for seeds over a period of 20 days (an example of non-claustral colony founding behaviour).

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THE EFFECTS OF MAN MADE DISTURBANCE ON ANT AND VEGETATION DIVERSITY IN FORESTS AND SAVANNAS

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The effect of man-made disturbances on ant and vegetation diversity in forests and savannas was evaluated. Forests sites disturbed under the 'slash and burn' regime and in different stages of recovery were compared with virgin forest in San Ignacio de Yuruani (Bolívar State) and El Merey (Monagas State), Venezuela. Savanna sites that had been used in the past as small roadways and that had been abandoned at different times were compared with virgin savanna in Canaima (Bolívar State). The ant fauna in the forest and savanna sites was sampled using pitfall traps at intervals of 10m along a transect of 180m. The vegetation was sample by estimating the number of morpho species, equitability and the coverage at each site, in the forests along transect of 10m² and in the savanna in quadrats of 0.25m². In San Ignacio the ant fauna was not affected whilst in El Merey noticeably impoverished. The vegetational diversity at these sites did not recuperate, although there was a certain degree of recuperation as regards coverage. The ant fauna in the savanna sites was not greatly altered by the roadways; the vegetation, however, did not recover either in diversity or in coverage. The species diversity of both ants and plants shows that a complete recovery is not obtained - a reflection of the irreversibility of ecological processes.

THE ROLE OF ANTS ESOPHAGUS IN THE TROPHALAXIS (FORMICIDAE)

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Usually the esophagus is considered a narrow tube connect the pharynx to the crop and this last one as a principal region of the digestive tract involved in the trophalaxis, like a pump. Esophagus of *Monomorium pharaonis* (queens and workers), *Crematogaster* sp (workers) and *Pheidole* sp (major and minor worker) were studied under SEM. The esophagus of these species presents a strong circular outer musculature which is arranged obliquely when it is empty, in turn, the crop presents few thin muscle fibers projecting in various directions without a definite arrangement. In base of these data, we believe that the esophagus have a pump function and the crop would be a simple reservoir. The pharynx muscle, by contraction or relaxation may act in retaining the contents of the esophagus. The esophagus, now empty, by distention of its circular muscles may create the negative pressure needed to pull of the food contained in the crop. The slight pressure on the crop content by the action of its muscle and distended wall may yield part of its content to the esophagus. Contraction of the strong musculature preceded by relaxation of the pharyngeal muscles may expel the esophageal content. By this point of view the esophagus function may be compared to the pump, aided by a strong muscle present in its wall.

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THE APOCRINE SECRETION IN ANTS *Pachycondyla striata* VENTRICULUS (FORMICIDAE:PONERINAE).

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The epithelium of the ventriculus of *P. striata* consists of high cells (digestive cells) with a centrally positioned nucleus and with an elongated and dilated apex. Countless formation of structures described by Caetano (1988) as globet cells are noted among these cells. These formations result from the joining of the apical portion of 2 or 3 cells. At the base of these cells there are the generative cell in various stages of development always developing two by two. The basal portion of the digestive cells shows large numbers of invaginations, which are irregular in shape and quantity. At the apical portion these cells form elongated club-shaped processes which eventually detach and are released into the lumen of the ventriculus in the form of small spheres indicating the apocrine type secretion. These spheres usually present the microvilli of the cells that produced them. Upon release into the lumen, these spheres migrate intact to the central portion where they encounter the peritrophic membrane and pass still intact into the space limited by this membrane and proceed towards the central region where they are detected in different stages of lysis. This apocrine secretion may prevent the enzyme present there from attacking the apex of cells other than those specialized and may also prevent dilution of the content and the consequent reduction in efficiency. The release of the content into the space delimited by the peritrophic membrane demonstrates 5 facts: 1. this is the site of action of the content of the spheres; 2.. the peritrophic membrane is inert to the action of the content of the spheres; 3. this space must contain the factor responsible for lysis of the membrane surrounding the sphere for release of shpere content; 4. the peritrophic membrane acts as a barrier preventing the substance responsible for shpere lysis from attacking the ventricular epithelium, thus performing a protective function for the cells of these epithelium and 5. the substance that lyses the spheres must be of extraventricular origin.

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THE DIGESTIVE TRACT OF THE *Catalaucus* ANTS: PRESENCE OF THE MICROORGANISMS IN THE ILEUM.

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Cataulacus ants present many similarities with neotropical ants from Cephalotini tribe. These similarities are recited to: behaviour, external morphology and use of trees to construct their nest. By other hand there is no information about their internal morphology, as we have found for Cephalotini ants. In this investigation we used queens and worker of *Cataulacus* from South Africa, preserved in Dietrich fixative. The digestive tract was removed, prepared for histology in usual method for parafin inclusion and stained with H-E. The digestive tract is quite similar to that found in Myrmicinae subfamily. They do not have a proventriculus bulb, but the ileum presents ligh dilatation in its proximal region. This region is full of microorganisms, similar to that found by us in *Zacryptocerus*, *Cephalotes* and *Procryptocerus* ants. The rectum presents three circular rectal pads in the anterior portion, like others ants from the Myrmicinae subfamily.

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FAPESP, CNPq, FUNDUNESP.

TROPHIC AND REPRODUCTIVE EGGS IN WORKERS OF *Neoponera villosa* ANTS (HYMENOPTERA: PONERINAE)

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In Hymenoptera, workers are not considered to be females responsible for reproduction within the colony, this task belonging exclusively to queens (BELL and BOHM, 1975). However, egg laying by workers ants has been reported with a certain frequency. Scanning electron microscopy has revealed the presence of two types of eggs in *N. villosa* workers: a) eggs with normal oogenesis and vitellogenesis and chorion deposition (probably the eggs of abnormal aspect in which vitellogenesis was probably interrupted and chorion deposition did not occur (oocytes in the reabsorption process). These abnormal oocytes were detected in workers age 25, 30 and 40 days, presenting sharply altered morphology and irregular contours, a fact not observed in normal oocytes. Histologically, these eggs are highly vacuolized, with vacuoles irregularly distributed throughout the cytoplasm and vitellus of disorganized aspect. The follicular epithelium, in addition to presenting cell degeneration, appears to undergo stratification. Transmission electron microscopy permitted us to observe that these oocytes in reabsorption contain large amounts with lipids. Large amounts of electron-dense bodies are observed interspersed with these lipid spheres. The presence of corpus luteum was observed in only one worker, suggesting the abnormal eggs may probably go through a partial reabsorption process, being then oviposited and utilized as food by the colony, thus corresponding the trophic eggs produced by workers.

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ULTRASTRUCTURAL STUDY OF THE FOLLICULAR EPITHELIUM IN OOCYTES OF *Neoponera villosa* ANTS (HYMENOPTERA: PONERINAE).

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Insect oocytes are enveloped by the follicular epithelium. A series of functions have been attributed to follicular cells, like vitellin membrane and chorion synthesis and the transport of hemolymph products into the oocyte. Workers of *Neoponera villosa* ants aged 5, 15, 25, 30 and 40 days, as well as winged females and fecundated queens, were dissected and the ovaries removed and processed for transmission electron microscopy. *Neoponera villosa* workers aged less than 10 days do not present the formation of ovarian follicles (oocytes, nurse cells and follicular cells), indicating that vitellogenesis starts at approximately 10 days of age. Camargo-Mathias (1993) was established that the follicles in ovaries of *N.villosa* are presented in 3 stages, where in stage I the nurse chamber is larger than the oocytic one, in II they present oocytic and nurse chambers with similar size and in III the oocytes are larger than the nurse chambers. In *N. villosa*, the follicular epithelium of stage I oocytes does not present the opening of intracellular spaces. In stage II, these spaces begin to be observed at considerable frequency, forming a space through which the hemolymph and proteins have easy access to the oocyte surface. In stage III two types of material were observed in the intercellular spaces. In the basal region there is electrondense material of flocculent appearance, and in the apical portions and in follicular epithelium-oocyte interface there is material with a compacted appearance and greater electrondensity. These observations lead us to conclude that the extra-ovarian material that reach through the intracellular spaces, with the follicular epithelium thus acting as a barrier of regulable permeability which determines the flow and types of protein incorporated into the oocyte.

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LA «GUERRE PHEROMONALE» DANS LES NIDS DE FOURMIS (*CAMPONOTUS CRUENTATUS*)

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En élevant une colonie orpheline de *Camponotus cruentatus*, l'auteur a observé la dynamique d'apparition des membres de la colonie. La colonie de *Camponotus cruentatus* a été établie le 8.4.91 en regroupant l'ensemble des larves hibernantes, des ouvrières de petite caste et un petit nombre de soldats. La colonie redevint normale en formant une des inter-castes fonctionnelles, qui ont été fécondées les 22, 23, 24 et 25.6.91 (les mâles sont très agités dans le nid, et la fécondation s'opère à l'intérieur du nid souterrain). Des oeufs fécondés sont nées toutes les castes de femelles, et des reines ailées en 1992. Lorsque les spermatozoïdes ont été épuisés, les inter-castes ont donné des oeufs de mâles et de soldats (comme cela se produit dans les colonies orphelines). Les six reines ailées acceptées par la colonie, montrent des occupations différentes. Les unes fonctionnent comme des soldats, bien qu'elles soient morphologiquement des reines, les autres se comportent comme des individus importants de la colonie. Ce travail a démontré que cette «élite» contrôle les castes en formation et aussi leurs fonctions dans la société. Nous pouvons conclure que la caste royale parfaite apparaît seulement avec l'absence de deux groupes de phéromones : les Phéromones de Caste Royale et les Phéromones Royales. Les Phéromones de Caste Royale contrôlent la morphologie de l'insecte et les Phéromones Royales leur fonction. Comme les soldats sont anatomiquement proches des reines morphologiques, ils pourront contrôler le développement des castes et leur fonction s'ils appartiennent à «l'élite» de la colonie, puisqu'ils auront la fonction des reines actives. L'auteur a déjà constaté des cas identiques chez les fourmis *Messor sp.*, *Aphaenogaster senilis* et *Camponotus sylvaticus* où le même fait s'est répété. Ce phénomène est aussi présent chez les autres Insectes Sociaux comme, par exemple, les méliponines (*Melipona quadrifasciata*, *Plebeia remota*, *Tetragonisca angustula*), les *Bombus*, les termites... mais avec leurs propres règles.

LES EXPOSITIONS D'INSECTES SOCIAUX

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Plusieurs dispositifs d'expositions permettant d'étudier les Insectes Sociaux sont présentés. Nous avons créé «l'Insectozoo», un insectarium pour les Insectes Sociaux dans une maison (Vila Ruiva, Rua 5 de Outubro n° 40, 7940 Cuba, Portugal). Ce musée est près d'Alvito au Sud du Portugal. Cette réalisation permet aux étudiants, aux scientifiques, et à toutes sortes de visiteurs (individuels ou collectifs), de prendre connaissance de la vie complexe des sociétés d'insectes (Isoptères, Hyménoptères). Dans ce but, sont créées des expositions qui donnent au visiteur la possibilité d'observer l'intérieur des nids. Bien que les nids des insectes présentent de fréquents changements occasionnés par le développement des sociétés qui y vivent, les dispositifs présentent une vision parfaite de leur architecture. On souhaite aussi illustrer l'évolution des espèces pour que le visiteur comprenne comment les sociétés complexes d'insectes ont évolué à partir des insectes solitaires. Pour obtenir une vision définitive pour une espèce déterminée, trois étapes différentes sont nécessaires et exigent trois types d'expositions différentes - (1) pour l'étude de la nourriture et du comportement social de la colonie - (2) pour l'étude de l'architecture du nid - (3) exposition définitive qu'on souhaite perfectionner au cours des années. Un exemple d'une exposition définitive est le «Formigueiro Messor» de 1989 du Centre Artistique d'Enfants de la Fondation Calouste Gulbenkian (Lisbonne) où une colonie de *Messor* de 1988 demeure encore vivante et en activité.

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YEASTS, BACTERIA AND SUGARS IN ATTA SEXDENS RUBROPILOSA NESTS

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The ants from the genera *Atta* cuts the leaves (Martin et alii, 1975), gathers its sap (Littledyke & Cherret, 1976) and use the remainder organic material for bulding their garden. The garden harbors bacteria, yeasts and a symbiotic filamentous fungus. The fungus associated with *Atta sexdens rubropilosa* ants metabolizes cellulose (Anversa et al., 1993). Several bacteria species also have cellulases (Bisson & Chambliss, 1989), but yeasts usually need simple sugars, mono- or di-saccharides, for growing. This work presents the determination of the amount of bacteria and yeasts and the characterization of simple sugars in the gardens from an *Atta sexdens rubropilosa* nest. Our results have shown averages of 3.6×10^5 bacteria cells and 2.7×10^4 yeast cells per grame in the ants garden. The leaves provided to ants as the sole food source contain glucose, fructose and probably sacarose. Organic material from garden, wich contains the associated microorganisms, presented glucose and cellobiose, indicating cellulase activity. So, both ants leaf-cutting action and microbial cellulose degradation can generate available simple sugars for yeasts development in nests.

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EXPLOITATIVE COMPETITION BETWEEN THE ARGENTINE ANT AND NATIVE SPECIES IN A PINE FOREST OF SOUTHWESTERN SPAIN

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Since its introduction into Spain, the Argentine ant (*Linepithema humile*), has been spreading rapidly. This is attributed to its high reproductive potential, its aggressive behavior and its efficient foraging and recruitment abilities. Although urban and agricultural consequences of this invasion are well documented, ecological effects are still poorly understood in the mediterranean area. In this work, we present the results of the competitive relationships *L. humile* establishes with other ant species in a National Park in south-west Spain. Exploitation of food resources by *L. humile* and other species of native ants was studied using three methods: 1) the use of attractive baits, 2) aphid-tending in pine trees and 3) prey finding. The Argentine ant occupied 94% of the pine trees, 49% of the baits and located 96.6% of the prey, in the zone it occupied. All of the native species in an adjacent area, occupied 46% of the pine trees, 33% of the baits and located 52.4% of the prey. However, the major use of the resources by the Argentine ant does not indicate that it is a more skillful species in occupying baits and in locating prey, if we consider the density of individuals. When the native species overlapped with *L. humile*, not only did their density decrease but there were changes in behaviours related to their foraging strategy.

VISUAL PERCEPTION IN *BOMBUS TERRESTRIS* L. (HYMENOPTERA APIDAE): CAN THEY GENERALIZE?

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Honeybee ability in recognizing figures of different form is well known (von Frisch, 1914; Hertz, 1934; Celli and Lazzari, 1992) while very few is known about bumblebees visual perception (Kugler, 1943).

This study aimed to investigate their ability to generalize some characteristics of the figures. We trained one worker per time to take sugar solution through a capillary. In the first test the bumblebee was offered the choice between a star (with sugar solution) and a circle (with water). Then, a series of tests were carried out in which the figures were substituted: *a*) the star was substituted with a figure made by five segments, then reduced to four, three, two, one and finally with a figure made again by five segments (all these figures offering sugar solution); *b*) the circle was substituted with a series of different figures, which always had a continuous perimeter (all these figures offering only water). Each test consisted of 70 visits; the first figure the bumblebee landed on at its arrival at the experimental desk was recorded. The relative position of the figures was changed at every visit, and the paper sheet was changed every five visits. The data show that the bumblebees were able to follow the scomposition of the star in a figure made by segments, and to follow its simplification. In fact, the percentages of right chooses in the first ten visits are high, and the trend of the tests do not resemble a learning process. Anyway, the test with one segment proved to be the most difficult, probably due to the decreased attractiveness of that figure when compared to the others present at the same time on the experimental desk.

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PETAL CONSUMPTION BY SOUTHERN SPANISH ANTS

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Ants considered as a whole are a very omnivorous group that feed on many kinds of food, either solid or liquid resources, animal or plant remains. As far as plant materials are concerned the majority of ant species extensively consume plant exudates and sap (which are obtained from both floral and extrafloral nectaries), honeydew produced by aphids, and scale insects, and seeds. Petal collection was initially considered as a very uncommon phenomenon, because petals and whole flowers were very rare in the diet of most ants. Nevertheless, previous observations in southern Spain showed that petals of *Halimium halimifolium* (Cistaceae) were a significant proportion of the items brought to the nest by foragers of *Cataglyphis floricola*, and were even preferred to insects when they were offered at the same time (Cerda et al. 1992). Later on, the same pattern has been found in other ant (*Aphaenogaster senilis*, *A. iberica*) and plant species (*Fumana* sp., *Helianthemum* sp., Cistaceae). This lead us to conclude that petal collection by ants is more common than expected in these regions.

Several authors doubt about the importance of petals as a food resource, and consider that collection of petals is du merely to individual mistakes of workers. Nevertheless, our observations about *C.floricola* and *A. senilis* nests cultured in laboratory conditions clearly demonstrate that petals are carried by workers as the other prey, and both larvae and workers chew them, even when they are already dry. Future studies should try to analyze the chemical compounds responsible of the ants attractiveness to these petals, and its possible role in ant-plant interactions.

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SPLIT SEX RATIOS IN THE ANT *LEPTOTHORAX ACERVORUM*

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Sex ratio theory deals with the evolution of allocation of resources to sexual offspring. Split sex ratio theory is a recent extension which considers how Hymenopteran workers are expected to bias the sex ratio of the colony's brood depending on the relatedness structure of the colony (Boomsma & Grafen 1990, 1991). *Leptothorax acervorum* is a British species of ant with one or more reproductive queens per colony, causing variable colony relatedness structure. If workers are in control of colony sex allocation (Trivers & Hare 1976), split sex ratio theory allows the calculation of the optimal sex ratio that workers are expected to produce. I am testing whether workers rear the predicted colony sex ratios; preliminary results indicate that they do. This work is an important test of current developments in sex allocation theory, and of kin selection theory in general.

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INTEGRATED PEST MANAGEMENT (IPM) AGAINST VARROA JACOBSONI, A PARASITIC MITE OF THE HONEYBEE APIS MELLIFERA

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Commercially available synthetic varroacides are able to limit the damages caused by Varroa. The is growing evidences however that they produce residues in wax and honey. The development of resistant Varroa strains is also possible. We present the results of a study on IPM conducted the past five years on about twenty colonies. It was possible to keep the Varroa population below damage threshold without the use of any synthetic acaricide. Our IPM method has a biotechnic part and treatments with formic acid. The biotechnical manipulations consist in the removal of drone brood witch is very attractive for Varroa and the formation of nuclei. The aim of those interventions is to slow down the development of Varroa population until treatments in fall. Two series of treatments by formic acid are made in August and September. Formic acid has varroacide properties and produces no residues in honey and wax. Counting the natural mite fall in October completes the method. This is a reliable indication about the remaining Varroa population in the colony (Imdorf, 1990). If the mite fall is more than one Varroa per day, a complementary winter treatment is necessary. By removing the drone brood we destroyed an average of 398 parasites per colony and year (min. 115, max. 775). We registered an average mite mortality of 1984 Varroas per colony and year due to formic acid treatments (min. 737, max. 6680). No important bee loss has been reported in connection with application of formic acid. The natural mite fall in October during this five years was far below one Varroa per day (means 0.10, min. 0.03, max. 0.21). No additional winter treatment was necessary.

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PRELIMINARY CLADISTIC ANALYSIS OF SOME NEOTROPICAL BUMBLEBEES USING MORPHOLOGICAL AND BEHAVIORAL CHARACTERS.

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The evolutionary history of the Neotropical bumblebees genus *Bombus* is being studied with special reference to the subgenus *Fervidobombus*, which is widespread in North, Central and South America. Morphological and behavioral characters are incorporated in a preliminary cladistic analysis. For the first time morphological character systems from females and males are used to produce a robust hypothesis of relationships. Special emphasis is given to the female sting capsule and seventh sternite because this study has proven them to be systematically informative. In addition, data on nesting habits for over half of the species is incorporated into the analysis. This is the first ecological information available for many little-known Neotropical species. A more detailed analysis of bumblebee nesting behavior and nest architecture may reveal whether tropical nest architectures are derived from patterns seen in temperate species, or the reverse.

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INTERACTION BETWEEN AGE AND FOOD FACTORS IN NESTMATE RECOGNITION IN THE ANT *TETRAMORIUM* *BICARINATUM*

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Kinship theory resulted in an increasing interest on kin recognition studies. Many of these studies evidenced correlations between relatedness and social discrimination.

In contrast, the present study was to investigate the influence of age and food factors on nestmate recognition and their possible interaction in different groups of workers proceeding from a same mother colony of the ant *Tetramorium bicarinatum* (this allowed to set up groups which are genetically proach). The discrimination tests were inspired from a scale proposed by Carlin and Hölldobler (1986).

For different age groups we carried out dyadic encounters between :

- individuals which have the same age and receive the same diet.
- individuals which have the same age and receive different diets.

Those tests were realized with ants of different ages.

Results showed that :

- ants displayed significantly more aggression behaviour toward individuals which received different diets, vs. individuals which received the same diet.
- the aggressiveness increased with age between ants fed with the same diet. Conversely aggressiveness declined with age and then became steady between groups which received different diets.
- there was an interaction between age and food factors.

These experiments on *Tetramorium bicarinatum* confirmed our hypothesis : food (environmental factor) and age (intrinsic factor) both influence nestmate recognition and they interact in the process of nestmate recognition.

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Foraging ecology of bumblebee species in Eastern São Paulo, Southern Brazil.

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The activity of visiting the flowers by two species of *Bombus* was studied in an area of gardens in São Paulo city, Brazil, during two consecutive years. During the first year, by the observational method, the species were detected on the flowers almost year around, except in June and July. During the second year by capture, the data showed that *Bombus morio* (n=88) interrupted its activity on the flowers from July to November and that *B. atratus* (n=15) was not captured in September, October and April. Considering the two years of study both species visited 41 botanical species that belong to 19 families. The botanical families most visited were Verbenaceae (represented by *Duranta repens*), Compositae and Leguminosae these with a greater number of species in the area studied. *Bombus morio* visited 24 species of plants and *B. atratus* 10 species and 6 species were visited by both species of *Bombus*. The results indicate that the species of *Bombus* are generalistics visiting lots of species of plants belonging to various families, of which some are looked for with more frequency.

CONTRIBUTION OF *TERMITOMYCES* FUNGAL ENZYMES TOWARDS CELLULOSE DIGESTION IN THE FUNGUS-GROWING TERMITE, *MACROTERMES BARNEYI*.

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Termites of the subfamily Macrotermitinae build nests containing up to several kilograms of fungus-gardens. These contain virtually pure cultures of the fungus *Termitomyces*, which grows on lignocellulose material collected by the termites. The termites then ingest the lignocellulose, together with the fungal mycelium and unique nodules of asexual spores produced by *Termitomyces*.

The role of *Termitomyces* fungus in the termite nest is controversial (Wood & Thomas 1989, Slaytor 1992). In this study, we investigated the hypothesis (Martin & Martin 1978, Martin 1991) that *Termitomyces* provides enzymes to facilitate cellulose digestion in termites.

Colonies of *Macrotermes barneyi* were excavated on the campus of The Chinese University of Hong Kong. Extracts of dissected worker midguts and hindguts were compared with *Termitomyces* nodules for enzymic breakdown of carboxymethylcellulose, avicel and cellobiose. Enzymic breakdown of 8 other oligo- and polysaccharides was also examined. Results showed midgut enzymic activity was considerably higher than in the hindgut. Major and minor workers showed very similar enzyme activities for the different substrates, indicating little division of labour for cellulose digestion among the castes. Specific activities (IU/mg protein) for carboxymethylcellulose, avicel and cellobiose breakdown were respectively 2, 5 and 44 times higher in the termite midgut than in the *Termitomyces* nodules. Similar higher activity in the midgut than the nodules was also found for other oligo- and polysaccharides tested. The results suggest that most of the enzymes for cellulose and other polysaccharide digestion originate from the termite and not from the *Termitomyces* fungus.

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SEPARATION OF NESTS AND INTRACOLONIAL RECOGNITION IN THE POLYDOMOUS ANT *CATAGLYPHIS IBERICA* (HYMENOPTERA, FORMICIDAE)

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The Iberian ant *Cataglyphis iberica* (Formicinae) is monogynous and polydomous. Numerous exchanges by mutual carrying are observed, especially just after the end of overwinter. These exchanges are carried out by some individuals of the colony forming a specialised subcaste of transporters (Cerda & Retana, 1992). We tested the effect of isolation of nests on intracolony recognition in *Cataglyphis iberica* by isolating individuals of three nests from the same colony during one year. The colony studied was without queen. After this period of isolation, no aggressive behaviour was observed when individuals of the nests were tested in pairs. However mutual investigations were significantly longer when partners were previously isolated, compared to control individuals from the same nest. This difference disappeared when individuals of the nests were reared together for five months. We analysed also cuticular hydrocarbons of workers collected in each nest: before, after isolation and after regroupment. The results showed: (1) that cuticular profiles were similar before and after regroupment of individuals (2) profiles had diverged after one year of isolation. This cuticular divergence seemed to be implicated in behavioural modifications (duration of mutual investigations) when partners met. Our results are in favour of the hypothesis that mutual carrying could permit the maintenance of a common odour among individuals of different nests belonging to the same colony (Cerda et al., in press).

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A PRELIMINARY INVESTIGATION OF THE DUFOUR'S GLAND SECRETION OF *POLISTES DOMINULUS* AND ITS SOCIAL PARASITE *POLISTES SULCIFER* (HYMENOPTERA: VESPIDAE).

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The function of the Dufour's gland in the social wasps has not been investigated deeply. Indeed, despite the amount of chemical work done on ants and bees, until now the Dufour's gland secretion has been analysed only in two species of social wasps belonging to the subfamily Stenogastinae (Keegans et al., 1993). In the subfamily Polistinae, most of the knowledge about this gland comes from work done on *Polistes fuscatus*. On the base of morphometrical data, Downing and Jeanne (1983) suggest that the Dufour's gland is involved in the communication of hierarchical status as well as in the production of substances that, once applied to the eggs during oviposition, are used as cues for their recognition by the foundresses of associative colonies. In the course of behavioural experiments, Dowling (1991) found no evidence that the Dufour's gland secretion played a role in dominance communication; however it seems to be involved in the recognition of the eggs. In the subfamily Vespinae, some social parasites have bigger Dufour's glands than their host species, suggesting that this gland could have some function in the control of the host colony (Jeanne, 1977; Landolt and Akre, 1978; Reed and Akre, 1982). In the course of this work the Dufour's gland secretion of *Polistes dominulus* and of its obligate and permanent social parasite *Polistes sulcifer* was analysed by means of gas chromatography-mass spectrometry. A complex mixture of n-alkanes, n-alkenes, mono- and dimethyl-alkanes ranging from C₂₅ to C₃₇ was found in the secretion of *Polistes dominulus* foundresses, the major components being 11- and 13-MeC₂₇, 11-, 13- and 15-MeC₂₉ and 11-, 13- and 15-MeC₃₁. We confirmed that this same mixture is present on the cuticle of this species, as found by Bonavita-Cougourdan et al. (1991). Both the Dufour's glands of the usurping parasite female and those of her newly emerged offspring contain the same hydrocarbons as found in the host, and the patterns of the two species are very similar. Further analysis are necessary in order to understand if this gland plays a role in the integration of *Polistes sulcifer* into the colony of the host species.

POLYGyny AND POLYMORPHISM IN A PONERINE ANT

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Centromyrmex bequaerti is an ant native to the equatorial forest who builds its nest in the termitaries of different species of *Cubitermes*. When the termitaries are broken open, it can be seen that the societies of *Centromyrmex* occupy different chambers and galleries of the termitary. These societies are polygynous and can have up to six queens; however, it is rare to find several queens in the same chamber. These queens have a morphology which is highly differentiated and are much bulkier than the workers who have a very distinctive polymorphism. A biometric study of diverse sclerotic elements in the workers shows a value distribution along unimodal curves. An analysis of polyethism as a function of polymorphism enabled us to establish that workers of different sizes can participate in hunting activities. Nonetheless, it seems the media are more involved in these activities whereas the major make up part of the nest's internal workforce where they play the role of guard. A study of predatory behavior clearly showed that *C. bequaerti* is a predator specialised in the capture of termites.

CUTICULAR HYDROCARBONS IN HONEYBEE UNDER NATURAL CONDITIONS

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Polyandry of the queen led to the coexistence in the honeybee colony of a large number of subfamilies (around 12-20 patriline). Several studies have demonstrated recognition abilities between super sisters (same father) and half sisters (different father) (Getz and Smith, 1983) and that cuticular hydrocarbons seem to function as labels during kin recognition (Page et al. 1991). However these studies have 2 limitations: the colonies contained only 2 patriline (instrumentally inseminated queen by only 2 drones), and the analysed workers were reared outside the colony. To know what happens in natural conditions, we conducted experiments with workers which were the progeny of a naturally inseminated queen (16 patriline). The characterization of the patriline of each worker was achieved by using nuclear markers, the microsatellites (Estoup et al., 1993). The cuticular hydrocarbons were compared in 3 sets of 5 day old workers:

- workers maintained in normal conditions (in their hive) = "hive bees"
- workers in groups of ten = "grouped bees"
- workers isolated since their emergence (without any contact with their congeners) = "isolated bees".

We hypothesize that, in the "isolated bees", the hydrocarbon composition has a purely genetic origin. However for the "grouped bees" and the "hive bees", the hydrocarbons could also come from the sisters. In addition for the "hive bees" they could come from the environment.

The hydrocarbon composition varied quantitatively between the 3 sets. For each compound, the variability is, generally, higher in the "isolated bees" than in the "hive bees", with the "grouped bees" being intermediate.

The question of whether to know if the hydrocarbon composition is characteristic of a patriline is being studied. At present, for the "isolated bees" and, at least for some patriline, it appears to be the case.

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GENETIC AND SOCIAL STRUCTURE OF THE LEAF-CUTTING
ANTS *ACROMYRMEX HEYERI* AND *A. STRIATUS*E.Diehl-Fleig¹, A.M.de Araújo² and S.Cavalli-Molina²¹ Lab.de Genética, Universidade do Vale do Rio dos Sinos
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The leaf-cutting ants *Acromyrmex heyeri* and *A. striatus* are very common in Rio Grande do Sul, Brasil and have been given a pest status. *A. heyeri* nests generally have a single chamber (2000-3000cm³) containing the fungus garden, queen, and immature and adult individuals. In contrast, *A. striatus* nests have several small chambers (5-150 cm³) at different levels, interconnected by channels. These chambers either contain the fungus, with or without immature and/or adult ants, plant material, and old substrate or are empty. In *A.heyeri* there is a temporal separation of adult males and gynes in each colony, although in *A. striatus* the males and gynes are present at the same time separated in different chambers. The time and pattern of nuptial flights are species-specific, and could be seen as strategies to reduce inbreeding. We analysed five loci (*Mdh-1*, ~~α~~ *Gpdh-1*, *Amy-1*, *Amy-2* and *Amy-4*) in 97 colonies of *A.heyeri* and 103 of *A. striatus*, from different demes and populations. Both species have high levels of gene diversities (*A. heyeri*: $H = 0,302$ and *A.striatus*: $H = 0,229$). The results suggest genotype-environment interaction, as the average gene diversity was lower in *A.striatus* with stable and permanent nests, than in *A.heyeri* with unstable nests. We found evidence of significant population structuration with the colony as the minor subdivision. Differences between nests were responsible for for the major proportion of variation at the species level: 45,1% in *A.heyeri* and 33,9% in *A.striatus*. Both species presents colonies monogynous and polygynous in all populations studied. The micro-geographic differentiation in allele frequencies possibly was due to stochastic processes, small effective size of demes and the low migration rates between them.

IS *BOMBUS TERRESTRIS* (L.) COLONY FOUNDATION FACILITATED BY THE PRESENCE OF VOLE (*MICROTUS ARVALIS* (PALLAS)) LITTER?

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Bumblebees are known to establish their colonies in old micromammals nests (Sladen, 1912). This observation has been confirmed by numerous authors (Alford, 1975, Heinrich, 1979). However, the underlying mechanisms of such a behaviour are unknown. Is that a more or less random choice, as suggested by Hobbs et al (1960)? Do the queen choose vole nests for size or microclimatic reasons, as suggested by Fye & Medler (1954)? Or are their choices ruled by pheromonal interactions with the rodents? This last hypothesis has been tested on *Bombus terrestris* (L.) and *Microtus arvalis* system. Founding queens have been installed in an air-conditioned room and submitted either to paper that had been previously used as vole litter or to an inert substratum only. After a few hours, the queens were observed to tear the soiled paper to pieces and use it to shield their first egg batch. Such a behaviour was never observed when the queens had inert substratum at their disposal. Further observations showed that the mean delay between foundation and egg-laying was 2 weeks for queens supplied with vole litter and 4 weeks for queens supplied with inert substratum. In conclusion, vole litter seems to accelerate colony founding in *B. terrestris*. Our best hypothesis is that there is an allomonal interaction determining the choice of the bumblebee queens for *Microtus* galleries and facilitating effect on the foundation.

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EFFECTS OF NEW JUVENILE HORMONE ANALOGUES ON CASTE DIFFERENTIATION IN *RETICULITERMES LUCIFUGUS*

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In the termite society the juvenile hormone titer and pheromones are important in caste differentiation (Lebrun, 1991). 6-[1-(2-phenoxyethoxy)ethoxy]-1,3-benzoxathiole (I) and four new derivatives, differing from it for the introduction of either a fluorine (II), a chlorine (III), a bromine (IV) or a iodine (V) atom in the position 4- of the phenyl, were synthesized and applied on *Reticulitermes lucifugus* to evaluate their juvenilizing activity. The products were supplied topically on thorax at the doses of 1.5, 3, 6, 12 and 25 µg contained in 0.5 µl of acetonic solution. After the treatment some groups of 30 pseudergates or 30 second-stage nymphs were placed together with a soldier in artificial nests. The products I and II at the dose of 1.5 µg transformed about 26% of the pseudergates into white-soldiers after 22 days, which successively became soldiers, and about 16% of the nymphs into adults with short and irregular wings and weakly pigmented integuments and eyes after 35-40 days. The products III, IV and V did not induce caste differentiation. At the other doses the 5 products resulted to be rather toxic. The products were less active than fenoxycarb, which is able to change the nymphs into white-soldiers in the field (Jones, 1989).

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SEXUAL BIOLOGY OF HAPLOID AND DIPLOID MALES IN THE BUMBLE BEE *BOMBUS TERRESTRIS*

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In *B. terrestris* diploid males develop normally into adults (Duchateau et.al.1994). Diploid and haploid males look very similar, but diploids are smaller than haploids. Also the size of the testis, expressed in size/radial cel is smaller. For both characters there is overlap in the frequency distribution. The spermatozoa of diploid males are larger than those of the haploids and the vasa deferentia contain far less spermatozoa than those of the haploid males of the same age. Countings and measurements of the spermatozoa, therefore, can give an indication about the ploidy of the males. Diploid males are successful in mating. They mate at a younger age than haploid males and they die sooner. The fecundity of diploid males, however, is very low. No queen, mated with a diploid male produced a colony, but a few queens produced some progeny. These might be triploid males and workers. In *B. terrestris* higher ploidy results in smaller individuals instead of larger, as has been found in several other species in the Hymenoptera.

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DIPLOID MALES IN THE BUMBLE BEE *BOMBUS TERRESTRIS* : SEX DETERMINATION, SEX ALLELES AND VIABILITY

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The frequency of colonies that produce diploid males after brother-sister (50%) and nephew-niece (37.5%) matings proves that in *B. terrestris* the sex is determined by a single multi-allelic sex locus. The diploid males which develop normally into adults make up 50% of the diploid brood. In the laboratory the growth rate of colonies with diploid males is influenced only slightly. Of 41 colony founding queens caught out of a natural population, all produced a colony without any diploid males. Therefore, the number of sex alleles in this population is estimated to be at least 24. This means that in commercial rearing systems for bumble bees, involving several generations, the occurrence of diploid males can largely be prevented by a good scheme for crossings.

MORPHOLOGY AND REPRODUCTIVE BEHAVIOUR OF INTERCASTES IN ONE COLONY OF THE PONERINE ANT *PACHYCONDYLA OBSCURICORNIS*

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Queens are the functional reproductives in *Pachycondyla obscuricornis* (Fresneau 1984), but none were found in one colony collected in Cerrado vegetation near Brasilia in 1992. However three adults differed morphologically from workers; although wingless, their thorax was more or less queenlike (metanotum larger than that of workers; scutum and scutellum distinct). Another 11 such individuals were found by opening cocoons, and we consider that they may be intercastes (*sensu* Peeters 1991). Two adult intercastes were mated and laid eggs (their ovaries contained dark yellow bodies). In contrast, all the workers were virgin, but some laid visually distinct trophic eggs which were given to the two reproductives.

Antennal boxing was observed between the mated intercastes, although they seemed equal in status. When we removed them, biting and jerking began among the workers, a hierarchy was established, and reproductive eggs were laid. The third intercaste (virgin) did not participate in dominance. When the mated intercastes were re-introduced (after 4 weeks), they initially became involved in attacks, but resumed their dominant status after a few days, and again monopolized reproduction. When the colony was dissected two weeks later, ovaries of the previously dominant workers were no longer active. The conditions in which the putative intercastes of *P. obscuricornis* are produced remain unclear. Distinct from ergatoid queens or gamergates, reproductive intercastes have never been reported in the Ponerinae.

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CASTE REGULATION AND DETERMINATION IN THE PHARAOH'S ANT *MONOMORIUM PHARAONIS* (L.): EVIDENCE FOR THE GENETIC DETERMINATION OF FEMALE CASTES.

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In the polygynic colonies of the pest ant *Monomorium pharaonis*, the presence of queens inhibits the production of new sexual (queen and male) brood. Moreover, eggs laid by extant queens act as a signal of their presence such that worker ants destroy sexual brood by cannibalism when this queen signal is present. Nevertheless, the capacity to produce sexuals is always present in the colony, since the removal of queens invariably results in the appearance of sexual brood. By analysing the time taken to produce sexual pupae in de-queened colonies, it has been possible to estimate that the age of these queen-potential larvae at the time of queen removal is only a few days. Consequently, the fate of queen-determined larvae in this species is either to survive to adulthood (which occurs only in the absence of extant queens) or to die by cannibalism in the presence of adequate numbers of existing egg-producing queens. Male larvae are treated by workers in exactly the same way. Since males are genetically determined by (haplodiploidy) and there is no convincing evidence that queen larvae are reared in any way that is quantitatively or qualitatively different from either male or worker larvae, the results of these various experiments provide evidence that female castes in this species are determined genetically by the presence of caste-specific genetic information contained within caste-determined eggs.

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Development of cephalic volatiles in young queens of the stingless bee, *Scaptotrigona postica*

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In stingless bees, queens are produced all year round. In the neotropical Trigonine *Scaptotrigona postica*, several of the large queen cells are usually constructed at the margins of the horizontal brood combs at any time, and gynes are emerging every few days. They stay in the corners of the brood nest and hide there because in strong queenright colonies young gynes are chased by the workers and usually are killed within 2 weeks after emergence. Only if the status of the colony allows swarming or supersedure, the young gynes have a chance to survive. If filial nests are available, a swarm may leave with one or a few virgin queens. Some days later the queens will start for a short nuptial flight. In the initial phase of the mating flight, the now receptive virgin will pass near a drone aggregation which had already formed some days earlier in the immediate vicinity of nests containing virgins. The drones recognizing the passing young queen at once become airborne and follow her. The queen usually disappears in the dense vegetation of the tropical rain forest. After some minutes she will return to the nest with a mating sign. In case of supersedure she still has to replace her queen mother. About 5 days after mating the queen is able to start egg laying. At an age of 25 days she has attained the full physogastric physiology of a dominant head of a colony. By means of gas chromatographic/mass spectroscopic analyses the pattern of cephalic volatiles was determined in pentane extracts of individual young queens of known age and function. Alcohols, ketones, esters, alkanes, alkenes and carboxylic acids were identified. 4 types of volatile patterns can be distinguished in the development of a young queen from emergence to dominance. Probably attraction of both workers and queens is released by an age-specific composition of volatile cephalic constituents. The potency of such specific pheromonal signals in the context of mating and dominance now can be bioassayed using blends of synthetic volatiles. Some of these biotests have already confirmed our hypothesis of age-dependent profiles of pheromonal messages representing important semantic elements in chemocommunication of social bees.

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HONEYBEES MEASURE DISTANCE OPTICALLY

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Honeybees communicate feeder distances to their hive mates in dances. Most experiments indicate that foragers assess distance by measuring the energy needed to reach a feeder (the "energy hypothesis"). We trained foragers to a feeding site suspended from a balloon at ground level, 70 m from the hive. It was then slowly raised straight up while bees continued to visit it. The distance between hive and feeder increased from 70 m at ground level to 114 m at the height of 90 m. Foragers also needed more energy to lift their bodies to the balloon. In spite of this, dancing balloon bees indicated 50 m at a height of 60 m, and 30 m at a height of 90 m. When compared with a feeder at ground level, individuals had to fly an additional 44 m to reach the feeder at a height of 90 m, and they had to lift their bodies up to 90 m. Energy expenditure increased considerably, but the distance perceived decreased by more than 50 %. The energy hypothesis cannot be correct. We propose an optical hypothesis: Retinal images of ground motion are used by bees to estimate feeder distance. The motion of retinal images decreases as foragers increase flight altitude. Bees do not have stereopsis, thus they cannot relate the decrease in ground motion to increasing flight altitude and underestimate distance.

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DIFFERENTIAL INTRACOLONY BROOD RETRIEVING IN ANTS *LEPTOTHORAX* (HYM. FORMICIDAE)

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Developmental stages represent distinct levels of energy investment in food, time and management by worker ants. A pupa costs more to produce than a larva and a larva costs more than an egg. Under a stress situation the protection given to eggs, larvae or pupae is expected to be proportional to the cost. Therefore, brood retrieval, as an aspect of that protection, should reflect this differential investment. We tested this prediction under the null hypothesis of no preference for eggs, larvae or pupae. Full societies of three *Leptothorax* species were used: *L. unifasciatus* (2), *L. tuberum* (2) and *L. nylanderi* (2). All members of the colony were dislodged from a nest tube and allowed to return inside the nest; each brood transport was noted. To maintain constant probabilities of items during the retrieval process each entering stage was replaced with a similar item; a repository of 20 eggs, larvae and pupae from the same society permitted this "sampling with replacement" scheme. Three up to six tests were run on a single day and colony but as each colony had a distinct composition, means for each colony are presented. In *L. unifasciatus* a sharp preference of predicted proportions was supported: pupae >> larvae >> eggs. A quality component seems to be involved. At a more refined level, a preference of big larvae vs. small larvae was not statistically apparent in *L. nylanderi* nor in *L. tuberum* nests. Similar data, usually in studies of brood pheromones, worker polyethism or colony emigration are sparsely found in the literature. Planned next steps are: i) test for preferences (3:1?) of workers on ♀:♂ pupae and ii) individual worker profiles in brood retrieving.

MORPHOLOGY AND ULTRASTRUCTURAL ORGANIZATION OF THE METAPLEURAL GLANDS IN CREMATOGASTER SCUTELLARIS (FORMICIDAE, MYRMICINAE).

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In *C. scutellaris* these glands have the typical morphology, a cluster of glandular cells and two chambers: the collecting sac and the reservoir. The ducts of glandular cells belonging to class 3 according to Noirot & Quennedy drain secretion and open themselves in cribrate areas of the collecting sac. As in *Myrmica rubra*, in *Atta*, in *C. clariventris* and *C. depressa* a narrow ridge occurs on the internal surface of the external wall of the reservoir. The ridge's function is related to the transport of the secretion by capillarity. The orifice looks like a slit due to the presence of a tegumental scale in front of it, bearing some long bristles on the lower margin. The ultrastructural organization shows a convoluted end apparatus. In the cytoplasm of the glandular cell there are many mitochondria oval, bell, cup, annular shaped, inclusions of lysosomal origin, smooth endoplasmic reticulum; moreover, near the microvilli of the end apparatus electron-dense inclusions occur, probably the secretion. According to these characteristics it is reasonable to suppose and intense secretory activity.

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COMMUNITY STRUCTURE OF HONG KONG ANTS

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Hong Kong has a significant area of protected grassland, scrub and forest, most of which has been subjected to centuries of human disturbance. Seventy sites representing different habitats and locations were sampled for ants using pitfall traps, baits and visual searching. Sites were sampled from June to September during the hot wet season when ants are most active. Ants were identified to species or morphospecies (approximately 150 species), and patterns of community structure were examined using Principal Components Analysis and Correspondence Analysis. Preliminary results indicated that community structure reflected vegetation type and degree of disturbance. Most ponerine ants were more frequent in forest, although *Diacamma rugosum* was almost ubiquitous. Fire-maintained grasslands were dominated by "tramp" species of dolichoderine (e.g. *Tapinoma* and *Iridomyrmex*) and formicine (e.g. *Anoplolepis*). Highest species diversity was found in established forest sites. The results will be used: to help distinguish centres of biological diversity in Hong Kong; to determine the existence and extent of different communities, with an assessment of the importance of "tramp" species; to infer the normal succession and facilitate biomonitoring of degraded and restored habitats; and to enable future study including that of species interactions and ecological role.

BEHAVIOURAL AND PHYSIOLOGICAL DEVELOPMENT IN *ECTATOMMA TUBERCULATUM* WORKERS (FORMICIDAE, PONERINAE)

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In *Ectatomma tuberculatum*, as in other monomorphic ants, polyethism is mainly associated with age (Dejean et al., 1989; Fénéron et al., 1989; Champalbert and Lachaud, 1990). During their adult life, workers pass through successive functional phases: inactivity, brood care, nest maintenance, guarding and finally foraging. This behavioural evolution appears to be closely related to physiological changes, as it was documented in other species (e.g., Fresneau, 1984). In *E. tuberculatum*, the workers' ovarioles grow progressively during the nursing stage, then regress and finally degenerate during the outside activity stage; the size of their poison gland increases continuously until workers become foragers. Based on individual marking and taxonomic methods, our results show also: 1) an important variability in the behavioural and physiological profiles between workers of the same age; 2) significant correlations between behavioural data and physiological measurements for each of the five age classes studied (17, 30, 45, 95 and 125 days old). Such a developmental plasticity correlated to the physiological state might suggest the existence of an hormonal control of age polyethism, as it has been well documented in honey bees (Robinson, 1992).

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MATING SYSTEM OF ATTA SPP. LEAFCUTTER ANTS -
INTRA- AND INTERSPECIFIC VARIATION IN PROBABLE
CORRELATES OF REPRODUCTIVE FITNESS.

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The *Atta* genus (Formicidae: Myrmicinae) contains some of the most advanced ant species with respect to complexity of society and caste system. Monogyny is predominant in all species but one, and queens are known to be multiply mated with several males contributing sperm. Morphological characters (and sperm content of males) were studied in alate reproductives of *Atta colombica* and *Atta cephalotes* from Panama as well as in young foundresses of the former. Colony level variation with respect to investment (measured as dry weight) into different components of individual male and gyne size were found for both species. Sperm content was found to be negatively related to thorax fresh weight in *Atta colombica* males, suggesting a possible evolutionary tradeoff with respect to investment into two probable components of male reproductive success, insemination potential (i.e. sperm transfer) and flight/ dispersal ability (related to weight of flight muscles). Sperm content was not correlated to individual male size after removing the effect of colony differences for that character. Across colonies and species, however, a positive relationship was found between male sperm content and total body size as well as thorax size, suggesting that the energy allocated to individual males vary at the colony level, as well as at the species level. The intraspecific variation in sperm content of males and foundresses was found to be substantial. Average absolute mating frequency were larger than 1 in *Atta colombica* albeit prominently smaller than in *Atta laevigata* and *Atta sexdens* (both approximately 3; Corso & Serzedello, 1981, Kerr, 1961). This may be related to the much lower degree of sexual dimorphism found in *Atta colombica*. The estimates obtained, however, are minimum estimates of mating frequency. The effective mating frequency might be substantially higher due to unequal and submaximal sperm contributions by males.

CASTE DIMORPHISM IN *POLYBIOIDES TABIDUS* AND *P. RAPHIGASTRA*

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Social wasps present little morphological caste differences between queens and workers compared to ants and bees; a high degrees of caste specialisation has only been found in the subfamily Vespinae (Wilson, 1971). In the Polistinae, morphological differences between castes are very small or even absent. Among swarm-founding wasps the Neotropical Epiponini (Carpenter, 1993), present the highest social level: with large colonies composed of thousand of individuals. Among Epiponini the gaster is normally wider in queens than in workers, due to developing ovarioles, but other size differences also occur in the thorax, head and even exocrine glands (Jeanne, 1980). In the Old World tropics, *Polybioides* (tribe Ropalidiini) forms large colonies of up to 2000 individuals in *P. raphigastra*. Recently, in *P. tabidus* we observed a probable trail-pheromone releasing behaviour during swarm migration (Francescato et al., 1993). Unlike the Epiponini, *Polybioides* lacks Richards' gland which is the source of a trail pheromone in Epiponini. To verify any caste dimorphism in this genus we have studied two species: *P. tabidus* and *P. raphigastra*. Richards (1969) had already noted differences in wing length and in the first metasomal segment between queens and workers of *P. tabidus*, but morphological caste differences have never been reported in *P. raphigastra* (Pagden, 1958). Our measurements together with recent findings that *P. tabidus* queens differ from workers in long hairs on the eyes (Turillazzi et al., 1994), confirm the presence of a distinct morphological caste in this species. Queens have a longer and wider thorax, wider peduncle and longer wings than workers. Moreover, apart from the degree of ovary development, physiological differences also exist in *P. tabidus* in the size of Dufour's gland. This gland, which we hypothesised as being the source of the trail pheromone, is larger in workers than in queens. The queen caste is also evident in *P. raphigastra* as these females tend to be more reddish than the workers. Morphological differences exist in the wider gaster in queens which must contain a well developed ovary, and in the head-width that is significantly smaller in queens. These results add new information to the biology of this tropical genus and stress the differences and similarities with the Neotropical Epiponini.

ANTS AVAILABILITY AND THE DECLINE OF THE WRYNECK IN SWITZERLAND

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Beginning of the fifties, populations of the wryneck (*Jynx torquilla* L., Picidae) showed a steady decrease in Europe and particularly in Switzerland (Glutz von Blotzheim & Bauer, 1980). This bird, who is the only migrant species of the Picidae family in Europe, is mostly dependent on ants (mainly larvae and pupae) of the genera *Lasius*, *Tetramorium*, *Myrmica* and *Formica* for rearing his progeny (Hölzinger, 1992; Bitz & Rohe, 1993). Two hypotheses are proposed to explain this decline: the first one postulates that due to agricultural practices within the foraging territory of the bird (who is living in agricultural areas like orchards, meadows with scattered trees) ants populations also declined gradually. The second one assumes that ants populations are not declining but food accessibility is reduced because epigaeic nests are rare. To test these hypotheses we chose two study areas, one with a low bird density, the second one with a high bird density. Within the two study areas, ants population density, species diversity and density of epigaeic nests are compared. Preliminary results are presented and discussed.

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(1) part of a Ph D thesis at the University of Lausanne (Switzerland)

POLYANDRY IN HONEYBEE QUEENS MAY, BY COLONY SELECTION, LEAD TO BALANCED EQUILIBRIA IN PATRLINE SPECIALISATION

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In diploid organisms the composition of genetic material from two parents may cause balanced equilibria where genes, unfavourable if homozygotic, are maintained due to their advantage if heterozygotic. Honeybee colonies may be viewed as superorganisms with selection working on their properties, where fitness is expressed in terms of produced drones and swarms with queens. They are composed of workers descendent from one diploid queen but from about 10 to 15 different haploid drones. From the high number of 'parental' organisms, linked by the chance process of mating, the proportions of workers expressing specific genetic traits may vary in fine-graded steps between colonies. Colony fitness is likely to be affected by this variation in the quantitative composition of workers with different genetic traits. Computer simulations show that under a wide range of conditions, where a special trait is favourable if expressed by small proportions of the workers, but unfavourable if expressed by many or all, genes coding for that trait are maintained at equilibrium levels within a population. Under these conditions natural selection would establish genetically polymorphic drones and queens, which produce optimal colonies only in particular compositions of mates, but suboptimal in other compositions. The process resembles that of classical overdominance in that a proportion of colonies enjoy higher fitness at the expense of others with lowered fitness. It differs in that it may operate not only in recessive, but also in dominant genetic systems, with respectively higher or lower speed of propagation and equilibrium levels depending on the type of fitness functions assumed. By the high number of parental organisms it can react closely to complex relations between the composition of colonies from genetically different workers and colony fitness. It is thus not unlikely that this process plays some role for the establishment of the genetic component in the division of labour in honeybee colonies.

A STUDY OF SYMBIOTIC RELATIONS BETWEEN FORMICOIDEA (INSECTA: HYMENOPTERA) AND ZYGENTOMA (INSECTA: APTERYGOTA) IN SPAIN.*

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In this work we present the results of the study of many samples taken in various habitats characteristic of the Iberian peninsula and Balearic Islands, where we have found numerous myrmecophilous *Zygentoma*. Our aim was to determine which edafic Formicoidea admit these Apterygota in their nests, what was the degree of specificity between the associations, as well as to know in more detail the nature of these symbiotic relations. We collected more than 4000 specimens of *Zygentoma* (5 genera and 19 species) in 688 ant nests of 40 species belonging to 15 genera of Formicoidea. Despite the great number of nests studied, we did not find significant differences between the species of a genera, but we did between different genera. The 47.4 % of nests where we found *Zygentoma* belong to *Messor*. Other well represented genera are: *Camponotus* (12.6 %), *Aphaenogaster* (10.9 %), *Pheidole* (7.7 %), *Formica* (6.25 %) and *Tetramorium* (6.25 %). It was observed that the *Messor* ants behaved in a different way to the rest of the Formicoidea studied, accepting a great diversity of these Apterygota. Moreover of this genus, only *Aphaenogaster* and *Camponotus* showed a low specificity in the association. However *Messor* admitted a large number of species and specimens per nest. Out of 135 samples in which we found more than one species of *Zygentoma* per nest, 83 % of cases proved to be *Messor* ants.

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INTER AND INTRA LINEAGE MITOCHONDRIAL DNA VARIATION IN THE HONEYBEE *APIS MELLIFERA*

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Mitochondrial DNA (mt DNA) variability has been studied by RFLP analysis of 87 colonies belonging to 12 of the 24 acknowledged subspecies of *Apis mellifera* (Garnery, 1992). A total of 23 haplotypes have been detected which are clustered into three major phylogenetic lineages (M, A, C) corresponding to three groups of populations with distinct geographical distributions. These results partially agree with previous findings based on morphometric variation (Ruttner et al., 1978). However, a new evolutionary scenario of the species was proposed (Garnery et al., 1992) to take account of the coexistence of two distinct lineages on the Iberian peninsula (Smith et al., 1991). In order to increase the sampling, a simple test has been developed using restricted PCR-amplified mt DNA (Garnery et al., 1993) which combines the length polymorphism of the COI-COII intergenic region with a restriction site (*Dra*I) polymorphism. This test, now performed on more than 1000 colonies, differentiated 31 haplotypes (15 in lineages M and A and 1 in lineage C) providing new information about relationships within the western mediterranean area populations. For instance, it shows that honeybees from several mediterranean islands (Sicily and Greek islands) which have African mtDNA, are more related to honeybees of southern Spain than to North African bees. This test actually differentiates southern Spanish and African colonies including *A. m. scutellata*, which could be useful to confirm the maternal lineage of Africanized bees in America. Although it prevents any evolutionary study within lineage C, the existence of a single haplotype the length of which is minimal in this particular lineage addresses the question of the possible constraints limiting nucleotide variation in this intergenic region.

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MICROSATELLITE VARIATION AND SOCIOGENETIC ORGANIZATION OF CARPENTER ANTS (*CAMPONOTUS* SP.)

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The genus *Camponotus* is regarded almost exclusively monogynous. However, oligogyny, a special form of polygyny where the nest is spatially divided by a few queens, has been reported in *Camponotus herculeanus* and *C. ligniperda* (Hölldobler 1962). The studies of the colony structure in social insects are severely restricted because of the low level of allozyme variation in Hymenoptera. Therefore, microsatellite markers were developed for both *Camponotus* species and a small number of individuals (several/colony) were genotyped. In *C. ligniperda* one polymorphic locus was found with eight alleles and H_{exp} 0.74 in one population. *C. herculeanus* had two polymorphic loci, one with four alleles in one population and the other with eight in the pooled data from three populations. Unlike in *C. herculeanus*, in most *C. ligniperda* colonies workers could not be the offspring of a single reproductive pair. In most cases polygyny and polyandry could equally well explain the genotypes, but in three colonies of ten more than one reproductive queen was needed to explain the observed genotypes.

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HAFNIA ALVEI SEPTICAEMIA OF THE HONEYBEE, APIS MELLIFERA L.

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Facultative insect pathogens may initiate secondary infections in bees of immunity lowered by stress conditions. *Hafnia alvei* that occurs in man, animals and birds, in natural environments (soil, water) caused fatal septicaemia in two beeyards in Finland (Oulu region, 190 bee colonies). The first losses appeared by the end of March, they were cumulated during spring and ceased in the beginning of June. *Hafnia alvei* was present in the content of intestines, haemolymph, abdominal muscles of bees and in food stores. Stress conditions that resulted from *Nosema apis* invasion by altering the defense reactions of the bee enabled *H. alvei* to penetrate from the midgut into haemocoel, multiply in haemolymph and propagate in tissues. High mortality of *A. mellifera ligustica*, *A. m. carnica* and Buckfast points to a high pathogenicity of *Hafnia* isolates.

Viral infection, *Malpighamoeba mellifica* and *Acarapis woodi* invasion and pesticide poisonings as a cause of bee losses have been excluded.

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RESPONSES TO NOVEL INSECT PREY IN THE MYRMECIINE ANT *MYRMECIA NIGRICEPS* MAYR

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Predatory behaviour of myrmecine ants is very little known. The data obtained so far suggest that these ants are hunting strictly solitarily, and that they are detecting their prey visually. We studied the responses to various novel species of insects in captive colonies of *Myrmecia nigriceps* kept in large observation nests. In the majority of our tests we used a small colony of *M. nigriceps* in which all workers were marked individually. We used three species of novel potential prey: larvae of the Colorado Beetle (*Leptinotarsa decemlineata* Say), adults of the red firebug (*Pyrrhocoris apterus* L.), and larvae of the cockroach *Gromadorrhina* sp. The first two species are known to be well protected chemically against predators; the larvae of *Gromadorrhina* sp. are accepted readily as food by the ants. Insects belonging to a novel species were always very quickly attacked and retrieved to the nest by *M. nigriceps*. Inside the nest, the prey was always inspected by numerous ants. The larvae of *Gromadorrhina* sp. were relatively quickly given as food to the larvae of *M. nigriceps*, but Colorado beetles and firebugs were transported again out of the nest. Our data demonstrate thus that although *M. nigriceps* are hunting solitarily, the final decision whether to accept or to reject a given prey item is carried out on the society level: the prey brought to the nest by one worker may be transported away by another one. *M. nigriceps* were learning very rapidly to reject insects protected chemically against predators. That aversive learning was not visual, but involved the perception of chemical stimuli. Our data suggest also that *Myrmecia* ants may learn to avoid chemically protected insects inside their nest, as a consequence of contacts with the prey items retrieved by their nestmates.

FIELD EXPERIMENTS ON THE HOMING BEHAVIOUR OF THE EUROPEAN AMAZON ANT, *Polyergus rufescens* LATR.

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The obligatory slave-making ant *Polyergus rufescens* conducts raiding expeditions against colonies of the *Formica fusca* group. Raiders generally form close-packed columns moving with a straight route towards the target colony. Coming back home, raiding swarms follow exactly the same paths used during outbound trips. In order to investigate how *Polyergus* raiders orientate during their trips we carried out field experiments. Results suggest that the head of the raiding phalanx uses mainly visual (celestial) cues during the outbound trips. During the outbound journey raiders probably deposit a trail pheromone which functions as a chemical orientation cue on the way home. In the present study we also investigated homing mechanisms used by *P. rufescens* scouts whose role is to search for host colonies (Le Moli *et al.*, 1994). The exploratory paths performed by such workers consist in a twisted outbound route followed by a straighter return trip. Scouts were captured (just after they started the return trip), displaced in an unknown area and released. Directions they assumed well correspond to directions they were selecting just before the displacement. After release, they moved with a straight route until they reached the point where they expected their colony to be; there, they began to search for the nest entrances. These results suggest that *P. rufescens* scouts probably use a homing mechanism (path integration), similarly to that typically shown by individually foraging ants of the genus *Cataglyphis* (Wehner and Wehner, 1990).

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ANAEROBIC DEGRADATION OF LIGNIN METHOXYLATED MONOMERS BY A HOMOACETOGENIC BACTERIA ISOLATED FROM THE DIGESTIVE TRACT OF A WOOD FEEDING TERMITE *NASUTITERMES LUJAE*

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Termites harbour a large hindgut microflora which contribute in anaerobic digestion of organic matter. Although the cellulose metabolism is well-studied, lignin fermentation remains unclear and the total mechanisms involved in anaerobic lignin oxidation have not been elucidated. One simple approach to understand lignin metabolism under anaerobiosis is to investigate lignin monomer fermentation, e.g. with the use of methoxylated aromatic compounds.

In this study, an anaerobic bacterium which degrades lignin monomeric compound derivatives has been isolated from the hindgut of a wood-feeding termite, *Nasutitermes lujae*. This bacterium grows with methoxylated aromatic compounds. These compounds are used with a concomitant production of acetate as the only fatty acid end-product.

The isolate also converts the trisubstituted methoxylated cinnamic acids (3,4,5 trimethoxy or 3,5 dimethoxy, 4 hydroxy) into 4 acetate per mol of substrate degraded. In comparison to the benzoate derivatives having the same number of methoxyl groups (3,4,5 trimethoxybenzoate and syringate), 3 acetate are produced per mol of substrate degraded. Moreover, this homoacetogenic bacterium uses sulfide (mineral) or cysteine (organic) as a methyl acceptor thereby forming gaseous sulfur compounds including methanethiol and dimethylsulfide.

In case of the disubstituted methoxylated cinnamic acids (3,4 dimethoxy or 3 methoxy, 4 hydroxy) the strain only demethylates and oxidizes the lateral aliphatic chain. This biochemical process results in the production of catechol, acetate, methanethiol and dimethylsulfide of end-products. Their corresponding benzoate derivatives are fermented to catechol and acetate without any methyl sulfide compounds.

This bacterium could be affiliated to the genus *Pelobacter* due to its high G/C content in the DNA. Importance in the role of this bacterium in the metabolism of wood-feeding termites is discussed.

THE VULNERABILITY OF MYRMECOPHILOUS BUTTERFLIES IN BELGIUM

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The butterfly family Lycaenidae contains nearly 40% of all known butterfly species (Atsatt, 1981), their evolutionary success may be due to their various relationships with ants (Fiedler, 1991). The Lycaenidae represent 30% of the belgian butterfly fauna, and many of these species are threatened (Baguette & Goffart, 1991). Myrmecophilous butterflies of the belgian fauna tend to be significantly more vulnerable than non-myrmecophilous butterflies ($X^2 = 7.861$, d.f. = 3, $P < 0.05$; species were divided in four classes of vulnerability). Moreover, we assigned a degree of myrmecophily to each species (Bink, 1992), and calculated a Spearman rank correlation coefficient (degree of myrmecophily versus degree of vulnerability). Species which have closer associations with ants showed out to be more vulnerable than weakly ant-associated species ($r_s = 0.52066$, $P < 0.0011$). As highly myrmecophilous species are more specialized, they have higher habitat requirements. Thus, myrmecophily is an important ecological trait which should be considered in future butterfly conservation projects.

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MONITORING CHANGES IN GENETIC COMPOSITION OF A DEQUEENED *A.M.CAPENSIS* COLONY WITH DNA FINGERPRINTING

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In orphaned colonies of *Apis mellifera capensis* (Esch.) workers begin to lay diploid eggs about 7 days after queen loss. Some intriguing questions arise: Do workers of all subfamilies become egg-layers? Does egg-laying activity of subfamilies change over time? Do workers lay their eggs randomly with respect to the position in the hive or do they maintain territories? Does the colony raise the new queen from original queen brood or from worker derived brood? Which subfamily does the new queen belong to? An *A.m.capensis* colony was dequeened and capped drone and worker brood samples were taken. Nine days later an inspection of all combs did not reveal any queen cells. Twenty-one days after dequeening capped female brood was sampled at two different locations in the hive. After another 12 days an additional female brood sample was drawn. At this time one young queen was present in the colony and was sampled. *Hae III/(GATA)₄*-DNA fingerprinting was performed with individual bees as described elsewhere. Recent experiments showed that the female progenies of a single *capensis* worker have identical DNA fingerprint patterns (Moritz and Haberl, 1994). Workers of all three subfamilies determined in the original queen brood became egg layers. Furthermore, two additional rare subfamilies could be traced in the later samples. Egg-laying activity within two subfamilies differed highly significant over time. Samples from different locations in the hive did not reveal any significant differences in spatial brood distribution with respect to subfamily membership. Since no queen cells were found in the colony nine days after dequeening the new queen must have derived from a worker laid egg. Her DNA fingerprint pattern classifies her as a member of a very rare subfamily, thus proposing the possibility of a non-random mechanism for selection of the new queen.

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TERMITES AS PESTS OF WEST AFRICA UNIVERSITIES BUILDINGS

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Termite Damage to Buildings of Ivory Coast and Senegal Universities is examined.

We put in evidence six species of Dry - Wood Termite and Subterranean Termites belonging to three families : Kalotermitidae, Rhinotermitidae and Termitidae.

The Termite Damage has been controlled by insecticides.

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UNIQUE MODE OF STOMODEAL TROPHALLAXIS OF THE PONERINE ANTS *Hypoponera* sp. (JFC 11104)

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The stomodeal trophallaxis reaches its extreme development in ants, and it is fundamental to the organization of their colonies (Wilson 1971). However, in the Ponerinae, the existence of stomodeal trophallaxis is less certain and the habit is considered to be either absent altogether or else frequent but poorly executed in these ant group (Hölldobler, 1985). From our observations with Japanese *Hypoponera* sp. (JFC 11104) which produces both winged and ergatoid types of females and males, we are now able to add the positive record of the stomodeal trophallaxis in ponerines and observe that the adult casts possessed different trophallactic behavior each other, as follows. 1) The occurrence of trophallaxis was confirmed by the honeywater staining red dyestuff, where the staining contents of the crop demonstrated that liquid food stored in the crop was regurgitated to nestmates. 2) The trophallactic food exchange was not observed between worker and queen (except for callow queen), even though the colony had only one queen. The queens used the unique behavior to reject the soliciting of regurgitation by workers, which was called as "whipping" in this paper. 3) The observation with VTR indicated that worker spent much more time in the soliciting behavior of trophallaxis than did queen ones. (124 ± 143.8 (349 - 7) sec of workers vs. 18 ± 7.6 (40 - 7) sec of queens). Furthermore, the frequency of unsuccessful attempts on trophallactic food exchange (i.e. the solicitor failed to be regurgitated a droplet by the donor) between workers was higher than that between queens. 4) The trophallactic behavior of ergatoid queens was observed from 1 to 10 days after the eclosion, which indicated that the queens solicited and received the regurgitation of foods by workers until 8 days after eclosion, when they started to lay eggs. Since 8 days after eclosion, queens did not solicit the regurgitation by workers and displayed "whipping behavior" to workers because the worker started to solicit regurgitation by queens. 5) While winged males were only fed by workers, ergatoid males received food from workers and regurgitate it to callow queens, but not from queens and to workers. The ergatoid males possessed the long labium similar to those of workers and queens. Both in winged and ergatoid types, trophallactic behavior was never observed between males.

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THE EVOLUTION OF SYMBIOSIS OF TERMITES

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Ancestral termites could have ingested bacteria and protozoa along with dead plant material eventually leading to some of these microorganisms becoming resistant to digestion and establishing themselves as parasites which then evolved into symbionts. Termites with symbiotic cellulolytic protozoa are envisaged as evolving to increase their feeding efficiency on plant material. These termites, by natural selection, could then start acquiring their own cellulase activity to increase their cellulolytic capability but at this stage there is a potential conflict between the termites and the protozoa over their common food which could be resolved by eliminating the protozoa. The growing dependence of termites on cellulose would be paralleled with a dependence on nitrogen-fixing bacteria, because of the need for carbon-nitrogen balance. Such a scheme could account for the evolution of the higher termites. It would also suggest that in the present day lower termites, cellulolytic protozoa are apparently parasitic. There is considerable biochemical evidence to support this. All surviving termites, including the most primitive, *Mastotermes darwiniensis*, secrete their own cellulase. *M. darwiniensis* can also survive on starch in the absence of cellulolytic protozoa suggesting that they may be parasitic. The need for an endogenous cellulase must be largely due to the need for a source of glucose. The ancestral termite would not have been able to digest cellulose and would have had to survive on simple sugars. The acquisition of cellulolytic protozoa, which metabolise cellulose to acetate, would not have increased the availability of glucose for the termite. Present day termites are unable to synthesise glucose, which does not matter as they have their own cellulase, and are unable to convert pyruvate to acetyl CoA. Apparently this strategy is used to provide the bacteria with pyruvate for metabolism and is correlated with the ability of the termite to utilise acetate produced by the microorganisms. In the absence of pyruvate dehydrogenase activity, acetate produced by both bacteria and protozoa has become the main source of energy used by the termites. This could explain why even the higher termites can not survive without symbiotic bacteria. Protozoa can be eliminated as long as bacteria are kept to produce acetate.

THE LADY AND THE JANITRESS: COSTS AND BENEFITS OF CARPENTER BEE SOCIALITY

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Kinship, manipulation and the necessity to cooperate in nest defense may be coercing factors in the evolution of sociality. One way to obtain an insight in the impact of these factors in social evolution, is to analyse their influence on the costs and benefits of social nesting in facultatively social species.

The carpenter bee *Xylocopa pubescens* is a such a species. Social nests contain a reproductively dominant forager, and either a young pre-reproductive or a formerly reproductive guard bee. These formerly reproductive females remain in the nest after dominance has been taken over by either an intruder or a nestmate. After such a supersedure, the new dominant does not allow the old female to enter the breeding part of the nest, thereby offering her the choice to either remain in the nest-entrance or to leave the nest.

Here, the costs and benefits of guarding by formerly reproductive females is analysed, both from the point of view of the dominant female and of the guard. It is concluded that both guarding females and reproductive dominants obtain a net profit from guarding:

The presence of the guard allowed the dominant female to make more and longer foraging flights. This resulted in more eggs being laid. In addition, the guard protected the nest from pollen robbery.

The guard's profits are mainly indirect fitness benefits, accruing to superseded females that remain guarding for a relative. Although there is a probability to regain dominance, the average benefits of this possibility alone are not enough to outweigh the average benefits of leaving the nest.

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THE REACTION OF MICROCEROTERMES SP.NEAR DIVERSUS TO VARIOUS KINDS OF BAITS,

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Microeerotermes sp.near diversus occurs as a serious pest in agriculture and buildings in Tabas southeast of Iran.To find out a feasible,economic al and environmentally safe method for controlling the termite,different kinds of baits including currogated card-boards in P.V.C. tubes,hay in cans date-palm wood in P.V.C tubes , card board in cans and date palm wood in soil were tested . The currogated card -boards in P.V.C tubes with a lid was the most attractive to the termite therefore it - was chosen as a suitable bait to introduce the - slow-acting toxicants such as Borax and Boric acid to the termite colony .The rate of loss of baits caused by termite feeding is shown in table 1.
Table 1 - The rate of loss of different baits cau-
Sed by termite feeding within 6 weeks %)

Replication Treatment	1	2	3	4	Total	Mean
Currogated card-board in pvc tubes	80	100	100	100	380	95
Hay in can	0	0	0	60	60	15
date-palm wood in pvc tubes	40	20	80	50	190	48
Currogated card-board in can	0	80	100	100	280	70
date-palm wood in soil	50	30	30	80	190	48
Reference						

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ation of Disodium octaborate Tetahydrate as a woo-
d preservative or a bait toxicant against the Fo-
mosan and eastern subterranean termites 22nd Ann-
ual meeting of IRG on wood preservation Kyoto Japan

PROTEIN, FAT AND GLYCOGEN IN BEES (*APIS MELLIFERA CARNICA POLLM.*), WITH AND WITHOUT, AN EGG LAYING QUEEN

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Changes in the amount of open brood in honeybee colonies cause either shifts in the age when specific tasks are performed (caste ontogeny) or changes in the frequency and intensity, of task performance (Dreischer, 1956; Winston & Fergusson, 1985). To enhance understanding the regulation of individual lifespan in worker honeybees we investigated the effect of brood reduction on adult bees. Individually marked bees were introduced into 2 experimental and 2 control colonies. The development of open and sealed brood was measured and the colonies inspected weekly for determination of survivorship. Queens were caged to prevent egg-laying in the experimental colonies. After ten days experimental colonies lacked open brood whereas control colonies exhibited normal levels. Bees aged 6, 10, 13, 18, 23, and 34 days were sampled 15 days after confining the queen. Average life expectancy was enhanced approximately by 50% in bees which were young at the time of cageing the queen. There were no significant differences, in the amount of stored protein, triglycerides and glycogen in young bees (nurses). However in 18 and 23 day-old bees the stores were significantly higher in the experimental group, where they reached their highest values. Differences in body reserves were maximal between experimental and control middle-aged workers, and less so in younger and older bees. Workers (aged 6, 10, and 13 day) in the experimental colonies had significantly lighter intestines than similarly aged control bees, but this difference was not maintained in older bees. We conclude that this reduced weight is the result of decreased pollen consumption, which nevertheless seems to provide sufficient nutrients to gain full body stores.

We attribute the later maxima in bees of colonies with a shortage of brood to a delayed caste ontogeny, and the higher maxima, to a less intense rate of work. This enables the bees to survive for a longer period and to regain their capacity for broodcare more quickly.

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DWARF QUEENS IN NANNOTRIGONA TESTACEICORNIS (APIDAE, MELIPONINAE, TRIGONINI)

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Trigonini gynes are known to be reared in royal cells, where they receive a surplus of food, responsible for queen determination. Nevertheless, dwarf gynes were mentioned in *Cephalotrigona* by Nogueira-Neto, in *Plebeia julianii* (=nigriceps) by Juliani, in *Plebeia emerina* by Kleinert (p.c.) and in *P. remota* (in Engels & Imperatriz-Fonseca, 1990). In *Nannotrigona testaceicornis*, eight dwarf gynes eclosed from normal (=worker) brood cells in a comb that also contained a royal cell. They presented the same behaviour as normal gynes. External (4) and internal (4) morphologies were studied, and compared with those of queens reared in royal cells. The colony was swarming, and needed a surplus of gynes. In *Plebeia emerina*, the colony was also swarming when a dwarf gyne was observed. Some reproductive traits in Trigonini bees occur only in very short periods of strong colonies. Until now, examples of these phenomena are the male production by workers of *Friesella schrottkyii*, the dwarf gynes production in *Nannotrigona testaceicornis* and the special kinds of gyne production in *Frieseomelitta* and *Leurotrigona*.

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CELLULOSE METABOLISM PROCESS IN THE LOWER TERMITE *RETICULITERMES SPERATUS*

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It is now well established that both higher and lower termites produce their own cellulases. Yamaoka and Nagatani (1975) found that two cellulases were present in *Reticulitermes speratus*, a lower termite, one in the salivary glands and the other, of protozoal origin, in the hindgut. However, partially or completely defaunated termites do not survive on a diet of wood indefinitely. Why does lower termites depend on hindgut protozoa for survival on a diet of wood? We firstly analyzed the distribution of cellulases in the digestive tract of *R. speratus* and found that cellobiohydrolase was present only in the hindgut, while caboxymethylcellulase (CMCase) was present in both salivary glands and midgut. Gel filtration profile of CMCase from the latter organ was different from that given by the former. These results suggest the participation of the midgut in digestion of cellulose. Secondary, we partially purified CMCase from both organs and characterized their properties. Furthermore, we examined the contribution of the termite origin cellulase by using completely defaunated termites. Protozoa were killed by irradiation of near UV (main wave length being 352 nm). After that termites were reared in three conditions; starved, fed on wood and fed on cellulose powder. Cellulose powder fed-termites survived after the death of starved termites with retaining CMCase activity.

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FACTORS AFFECTING THE POLLINATORS, POLLINATION AND CROP PRODUCTION

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Parameters like parasites, diseases and pesticides poisoning are the major factors. Which are affecting the pollinators population, pollination and crop yield. Bee flora of pesticide contaminated was identified and determined the pesticide residue levels in pollen and nector of bee flora and its effect on plant-pollinator relationship. Observed the decrease in fruit and seed production. Total loss of honeybee pollinators in the selected disease infested areas was 85-100 per cent. The foragers returning with pollen load at infested colonies was less than that at normal colony. Evidently these factors reduces the honeybee pollinators, pollination and crop yield.

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COMPARATIVE MORPHOLOGY OF THE VISUAL SYSTEMS IN SOME WASPS AND BEES

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The following morphological features of compound eyes and ocelli have been assessed from 130 species of all important hymenopteran groups: the absolute size, the angle and distances between ocelli and compound eyes and the ommatidial density. In most species the lateral ocelli are sized equally to the median ocellus. In some species of Scoliioidea, Sphecoidea and Ichneumonidea there are striking differences: the median ocellus in some Scoliides is bigger in size than the lateral ocelli; in *Scolia trifasciata*, *Sphex maurus* the lateral ocelli are reduced. To the contrary, the lateral ocelli of the braconide wasp *Macrocentrus gibber* are bigger than the median ocellus. Furthermore, also the quantitative analysis of morphological features of the visual system opens some senso-ecological and evolutionary questions. For example, in Fig.1. the relative distance between the lateral ocelli *rel d* is correlated with the absolute width of the head *w* (*n*=20; mean errors are not visible). For the vespoïd and apoïd species considered here, this ocellar measure is lower in the bigger sized species. This negative correlation is only present, if the extremely sized species are included. Furthermore, the Vespoidea have lower distances *rel d* than the Apoidea (with the very exception of the evolutionarily young honeybee species *Apis mellifera* und *A. cerana* whose measure *rel d* is near that of vespines).

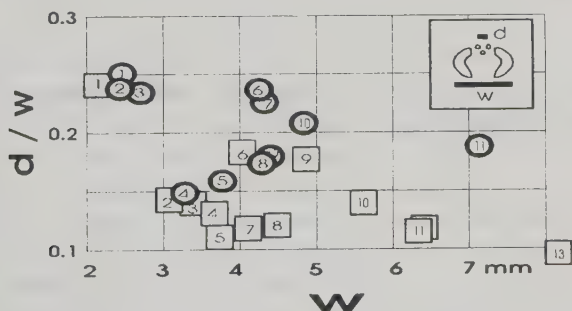


Fig.1. Correlation of the interocellar distance *rel d* with the head width *w*. Squares give Vespoidea: (1) *Celonites abbreviatus*; (2) *Polybia atra*; (3) *Polistes nimpha*; (4) *Dolichovespula saxonica*; (5) *Pseudovespa austriaca*; (6) *Eumenes unguiculata*; (7) *Belonogaster juncus*; (8) *Polistes hebraeus*; (9) *Eumenes maxillosa*; (10) *Paragris calida*; (11) *Vespa crabro*; (12) *Vespa cineta*; (13) *Synagris cornuta*. Circles give Apoidea: (1) *Halictus clavipes*; (2) *Apis florea*; (3) *Melipona ruficrus*; (4) *Apis indica*; (5) *Apis mellifera*; (6) *Sirex gigas*; (7) *Bombus lapidarius*; (8) *Apis dorsata*; (9) *Andrena funebris*; (10) *Psithyrus rupestris*; (11) *Xylocopa valga*.

Acknowledgments: Dr.M.Fischer. Nat.Hist.Museum, Vienna for leaving the exponents for investigation.

Nest usurpation and characteristics of the target nest in the subtropical paper wasp, *Ropalidia fasciata* (Hymenoptera, Vespidae).

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Nest usurpation in the subtropical paper wasp *Ropalidia fasciata* was studied in Okinawa, southern Japan. Most events occurred on late pre-emergence or early post-emergence colonies. A discriminant analysis showed that the usurpers preferred colonies that had fewer cells with abundant larvae and pupae, compared with average of unusrped ones on same date. After usurpation, eggs and larvae disappeared gradually, which were probably destroyed by the usurper. However, pupae remained in the cells until emergence and became workers after emergence. In eusocial wasps, nest usurpation is regarded as an effective reproductive strategy for a female that has lost her own nest. The usurpation, however, has certain risks for potential usurpers because it frequently involves a lethal fighting with regal nest owners. Thus, it is important for a potential usurper to select a target nest carefully. Nest preference shown by the usurpers suggested that they selected a nest that is easy to usurp (small nest) but has valuable resources (abundant larvae and pupae).

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**ORPHNEBIUS POLITUS CAMERON (COLEOPTERA:
STAPHYLINIDAE: ALEOCHARINAE), A SPECIALIZED
PREDATOR OF THE BAMBOO ANT *TETRAPONERA* SP.
(HYMENOPTERA: FORMICIDAE: PSEUDOMYRMECINAE)
WITH SUBSOCIAL BEHAVIOR**

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In contrast to the situation in many other subfamilies of ants, almost no myrmecophyles are known to be associated with the Pseudomyrmecinae, a taxon of almost exclusively plant-cavity inhabiting ants. During investigations on the bamboo ant *Tetraponera* sp. near *attenuata* I encountered a myrmecophilic staphylinid beetle, *Orphnebius politus* Cameron (Myrmedoniini), that exhibits an unusual biology in many respects. The tiny (ca. 3 mm) beetle waits near an entrance hole of a *Tetraponera*-inhabited bamboo internode until an ant emerges. It then quickly climbs onto the much larger (ca. 10 mm) ant's alitrunk, bites and chews at the articulation of the struggling ant's petiole, eventually paralyzing and killing its victim, presumably with the aid of poison from its abdominal glands. It then drags its prey to a safer place. Often already before the ant ceases to move, the beetle begins to walk about on it and "groom" its body surface and extremities. Commonly the beetle at some time begins to chew into the tip of the ant's gaster, pulling out the sting and feeding for some time at the inflicted wound. The beetle stays with its prey for a few days to well over a week, sitting on it and grooming it from time to time. Females may deposit an egg near the prey. After 3-4 days (25 °C, n=7) a larva hatches, which climbs about on the dead ant, grooming it and sucking in body contents of the ant where the cuticle is broken. In addition, the larva is fed and groomed by the female beetle, with trophallactic contact lasting for up to several minutes and accompanying swallowing movements in the gut of the semitransparent larva clearly recognizable. After ca. 3 days (n=6) the larva is fully grown and begins to search for a pupation site where to spin its larval shelter with silk from the abdominal tip. The female searches for new prey and, if successful, may lay a new egg within one day and raise a new larva. The mating behavior of *Orphnebius* was also observed. The male shows sexual pheromone calling behavior and may offer a dead *Tetraponera* as nuptial gift.

Relative abundance, seasonality and flower preference of Apid bees (Hymenoptera, Apoidea) in Eastern São Paulo, Southern Brazil.

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Relative abundance, seasonality and flower visiting by species belonging to the Apidae family were studied in an area within São Paulo city, with mixed vegetation composed of native and introduced plant species, where herbs and shrubs predominate, besides weed species. Analysis of samples obtained periodically during a year (July to June) through capture of bees on flowers showed a predominance of *Trigona spinipes* (Fabricius), *Apis mellifera* Linné and *Tetragonisca angustula* (Latreille) among the 14 Apidae species found. Other social bees species frequent in samples were all Trigonini, mainly *Paratrigona subnuda* Moure, *Nannotrigona testaceicornis* (Lepelletier), *Plebeia emerina* Friese, *Plebeia droryana* Friese and *Friesella schrottkyi* (Friese). Most species were captured all year round, presenting peaks of abundance related to favorable climatic and/or flora conditions. Although a great number of plant species was visited by each of the Apidae species, only few were intensively visited. From the point of view of resources use, these bees presented varied degrees of generalization. They also showed a tendency to concentrate on different botanic species, more evident among less taxonomically related species. Some floral preferences were highlighted by the great use of some plant species, independently of their abundance in the study area, and by greater foraging similarity among Meliponinae, specially those belonging to the genus *Plebeia*.

VARIABILITE MORPHOLOGIQUE ET POLYÉTHISME DES SOLDATS CHEZ LE TERMITE *MACROTREMES BELLICOSUS*

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Au sein des principales castes de soldats reconnues dans chaque espèce de termite, les auteurs ont observé une certaine variabilité morphologique. L'étude du polymorphisme de l'espèce *Macrotermes bellicosus* sépare des petits et des grands soldats, chez lesquels nous avons montré une variabilité liée à la coloration de leur abdomen et aussi à la taille de leur tête. Il est possible de distinguer des soldats à abdomen brun, à abdomen rouge, à abdomen jaune et des individus de coloration intermédiaire entre ces trois types. La dissection montre que cette coloration est due au contenu des réservoirs de la glande labiale. La répartition de ces différents types de soldats, entre l'intérieur du nid (endoécie) et l'extérieur (lieux de récolte de la nourriture), indique une plus grande proportion de grands soldats à abdomen brun (90,7 contre 64,6%) et de taille relativement plus grande ($p < 0,001$) à l'extérieur du nid. La répartition entre ces types morphologiques à l'intérieur du nid varie selon les perturbations: un nid soumis à des effractions répétées montre un pourcentage de soldats "bruns" nettement inférieur à celui d'un nid non perturbé (36,5 contre 64,6%). L'hypothèse la plus probable serait que cette coloration des réservoirs salivaires corresponde à un critère d'âge. Des résultats préliminaires étayaient cette hypothèse. Le taux d'acide urique est plus élevé dans la classe des "bruns" que dans celle des "jaunes" (2,17 contre 1,46 $\mu\text{mole/grand soldat}$). Egalement, la survie des soldats bruns semble plus réduite que celle des jaunes. Ces observations nous conduisent à envisager un polyéthisme lié à l'âge chez les soldats de *M. bellicosus*, tout comme chez les ouvriers de la même espèce. Chez les soldats de cette espèce, il existerait une variabilité morphologique selon leur localisation. Les individus (petits et grands soldats) qui assurent la défense à l'extérieur du nid lors de la récolte de la nourriture seraient de taille relativement plus grande et d'âge plus élevé que ceux restés à l'intérieur du nid.

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THE RELATIONSHIP BETWEEN VEGETATION TYPES AND ANT COMMUNITIES AT THE RIVERSIDE OF AGATSUMA-GAWA, GUMMA PREFECTURE, CENTRAL JAPAN

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Ant communities were studied by using a set of traps of one-third diluted honey at several vegetation of riverside of Agatsuma-gawa (530-650m), Gumma Prefecture, Central Japan. After 90 minutes of exposure, ants in the traps were sorted and counted according to species to make a diagnosis table as like as plantsociology. From the tabular analysis of 28 species and 89 sites, 4 types and 10 subtypes of ant communities were recognised by the indices of the coverage and the constancy. The coverage, defined as the extent of space covered by a species within a given area, were indicated arithmetically of the ratio of the traps occupied by exposed. At the vegetation of wetland type, there is *Lasius niger* community. At the vegetation of grassland type, there is *Lasius niger*-*Formica japonica* community (including *Myrmica jessensis* subcommunity, *Myrmica jessensis*-*Paratrechina flavipes* subcommunity and *Paratrechina flavipes* subcommunity). At the vegetation of woodland type, there is *Lasius niger*-*Paratrechina flavipes* community (including *Pheidole fervida*-*Myrmica jessensis* subcommunity, *Formica japonica* subcommunity, *Formica japonica*-*Pheidole fervida* subcommunity and *Pheidole fervida* subcommunity). At the vegetation of forest type, there is *Paratrechina flavipes*-*Pheidole fervida* community (including *Aphaenogaster japonica*-*Lasius niger* subcommunity and *Aphaenogaster japonica*-*Formica* sp.5 subcommunity). Each community seems to have two indicator species and two other subordinate species. These characteristics are common to the lowland fauna and the mountain fauna in central Japan.

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THE EFFECT OF EARLY ILLUMINATION CONDITIONS ON ILLUMINATION PREFERENCES IN THE ANT *CAMPONOTUS MELANOCNEMIS* SANTSCHI

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We investigated the effect of early illumination conditions on illumination preferences in the ant *Camponotus melanocnemis*. Foundress queens of *C. melanocnemis* were isolated in large test tubes and kept in constant darkness. After the appearance of pupae, two groups were created. Group I (15 queens) continued to be kept in constant darkness, group II (15 queens) was exposed to 12:12 LD rhythm. Workers which eclosed in each of the nests were exposed to either darkness, or 12:12 LD rhythm, during the first 3-4 weeks of their adult life. Then, the whole nest was again put into darkness, to assure that the possible effects of early exposure to light on illumination preferences of the tested ants involve phenomena more complex than simple transitory habituation to light of the ants exposed to 12:12 LD rhythm. After a month in darkness, the workers were isolated from their mother queens and from brood, and marked individually. After 3 days, groups of workers (2-6) descending from the same queen were put each into a double nest composed of a part exposed to 12:12 LD rhythm, and of a part kept in darkness (covered with a lightproof cloth). The ants were then observed 10 times a day during 40 days. During each test, we noted which ants were present in the illuminated half of the nest, and what was their behaviour. Although the ants of both groups stayed most frequently in the dark zones of their nests, the ants exposed to 12:12 LD during the first 3-4 weeks of their adult life avoided light highly significantly less strongly than the ants reared in darkness. We can thus conclude that early exposure to light may modify significantly illumination preferences of *C. melanocnemis*. These data confirm our earlier findings obtained in a similar experiment carried out using as subjects workers of the wood ant *Formica polyctena* Först.

EVOLUTION SAISONNIERE DE GROUPES TROPHIQUES DE TERMITES EN SAVANE PREFORESTIERE (LAMTO, COTE D'IVOIRE)

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Les termites de la savane de Lamto appartiennent à quatre catégories trophiques : les champignonnistes, les humivores, les xylophages et les fourrageurs (Josens, 1972, 1974). Les variations de biomasses de populations des deux groupes principaux (champignonnistes et humivores) ont été étudiées dans les milieux de savane herbeuse, savane arbustive et savane boisée. La répartition de ces groupes s'effectue selon un gradient croissant pour les champignonnistes et décroissant pour les humivores en fonction de l'importance des ligneux dans les biotopes. Les champignonnistes regressent en savane herbeuse et légèrement en savane boisée, relativement à la pluviométrie. Pour ces mêmes milieux, les humivores acquièrent des proportions de plus en plus croissantes. Les groupes évoluent différemment en savane arbustive, en indiquant que les champignonnistes augmentent en proportions, tandis que les humivores diminuent. Spécialement dans ce milieu, les xylophages se montrent plus importants en début de saison de pluie. Ces résultats font ressortir que les champignonnistes sont dominants dans les biotopes à forte production de litière (Kouassi, 1987 ; Lepage et Kouassi, 1989).

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MOLECULAR CHARACTERISATION OF AUSTRALIAN COMMERCIAL AND FERAL HONEYBEES

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The history of honeybee importations and management in Australia is largely anecdotal and therefore a survey and characterisation of this agronomically important insect is of obvious value. This research provides information on the genetic composition of 42 feral and commercial strains by sequencing sections of the ATPase 6, cytochrome oxidase III, cytochrome b and ND2 mitochondrial genes and determines the relationship of the lineages found to each other. Phylogenetic analysis shows novel associations between *A. m. mellifera*, *A. m. scutellata*, *A. m. ligustica*, *A. m. caucasica* and *A. m. carnica*, suggesting a possible alternative to the current hypothesis for the origin and evolution of honeybee populations. From an origin in the Middle East: one lineage spreads to the west splitting into two, one of which spreads further to the north; a second lineage spreads around the southern and western Mediterranean; and a third lineage spreads into sub-Saharan Africa. Also, the mode of sequence evolution is compared to that of other insects, in particular in terms of the unusually high numbers of transversions occurring in honeybee mtDNA.

INCORPORATION OF AMINOACIDS INTO PROTEIN UNDER ENVIRONMENTAL AND LABORATORY CONDITIONS

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Due to aging and the division of labour, each individual bee has changing protein requirements during its lifecycle. Very young bees need protein for growth, older nurse bees utilize large amounts to feed the brood, and forager bees require protein to maintain a high energy metabolism. Young bees consume more pollen than do older bees, but the latter receive additional jelly protein from nurses (Crailsheim, 1990, Crailsheim et al., 1992). The amino acid content of the haemolymph of forager bees is lower than that of bees which spend most of the day in the hive (Crailsheim et al., this volume). Whether the change in the amino acid content is due to differences in quality and quantity of consumed protein or the different life style is unknown. We used C14-phenylalanine as a tracer to investigate amino acid incorporation as a function of food consumption and lifestyle. Sister bees showed significantly lower incorporation rates of haemolymph amino acids into protein when kept caged in an incubator for the first 8 days of life (fed on honey or on caseine / sucrose) compared to those remaining in the colony. There were no significant differences in amino acid incorporation between colony bees and lab bees fed honey and bee bread whether or not brood were present. Food composition and environment strongly influence both amino acid composition in the haemolymph and protein metabolism of honey bees.

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POLYETHISM AND POLYANDRY IN HONEY BEE COLONIES *APIS MELLIFERA* WITH NATURAL MATED QUEENS

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Division of labour in honey bee colonies based on genetic differences between the patriline has been described in several studies in the last years. All of those studies share one major weakness: The colonies were headed by queens artificially inseminated with different mutant or allozyme marked drones. As a consequence, there are fewer patriline than in natural mated colonies.

The development of DNA-microsatellites for honey bees helps to overcome this difficulty. These hypervariable markers allows us to distinguish each patriline, even in a colony where the queen mated 19 times. We isolated DNA from worker bee heads and amplified it with the technique of PCR using carefully selected primers. This makes the assessment of each patriline's contribution in different task quick and secure.

The preliminary results show differences in the behaviour of the patriline: Nectar collecting bees, honey-capping bees, and bees getting groomed differ significantly from the control group.

Polyethism based on the genetic differences between patriline can be found in colonies with naturally mated queens. The microsatellite method has proven to be an efficient tool in the study of the complex family structure of honey bee colonies and the division of labour.

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**DESIGN AND ARCHITECTURE OF THE SUBTERRANEAN NEST
OF ODONTOTERMES HORNI (WASMANN) (ISOPTERA :
TERMITIDAE)**

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The vertical section of the subterranean termite nest included the distribution of various sized, shaped and numbered fungal chambers, in a multilocular fashion from 30 to 150 cm depth below ground level, in an area of 14.4 sq m. The smaller and broader chambers were situated in the peripheral and deeper area around the royal chamber, respectively. These were interconnected by galleries. The number of galleries varied depending on the size, location and function of the fungal combs. The royal chamber with finely plastered floor and dome to semicircular roof was located in the centre of the nest at a depth of 95.5 cm. Two layers of soil deposition were noticed above the roof. Interconnecting galleries were noticed in the royal chamber. Incubation cavities were situated below the royal chamber. Foraging galleries extended from the nest to the ground surface and varied in shape and size. Further, these were connected to the primary or secondary galleries located at 40 to 60 cm below the ground. Main depository fungal chamber was irregular in shape situated 16.5 cm away from the royal chamber.

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EFFECT OF INDIVIDUAL LEARNING PERFORMANCE ON COMPLEX ODOUR RECOGNITION IN THE HONEYBEE

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Olfactory learning abilities in the honeybee have been extensively studied using a conditioned proboscis extension (CPE) assay on restrained individuals. In most works the proportion of individuals eliciting the CPE is the only variable considered for data treatment. In order to investigate complex odour recognition in the honeybee, we considered the individual learning performances following two types of scoring. Bees were subjected to a 3 trial-training procedure (T) where the unconditioned stimulus US (contact of an antenna with a sugar solution) was associated with a conditioned stimulus CS (6 component-mixture) and the proboscis extension was rewarded by a food uptake. A blank trial (B) enabled to control responses to mechanical or solvent stimulus. Testing to the 6 individual components was then undergone. A final test to the CS was applied to control the persistence of the response (P). The scoring was based on the responses obtained at the T, B and P trials. From the 781 bees used in the experiment, 27 strategies were observed along the different trials. A first subjective scoring system assumed that the best conditioning was performed by bees exhibiting the CPE after one training trial (rapid acquisition), that did not respond at the B trial (specific response to odour stimulus), that still respond at P trial (persistent response), leading to 4 classes of bees : (I) best learners, (II) good level of conditioning but not specific to the CS, (III) no persistence of the conditioning, (IV) poor learners. A second system of scoring was based on a statistical analysis of the number of bees found in the different strategies. Responses elicited at the different trials, and their interactions, were considered as variables and ranked according to their respective contribution to the final effective of each strategy, which led to 3-4 classes of individuals, overlapping the classes previously defined. This convergence validates the biological interpretation used in the first scoring system. During testing, the best learners showed discriminative responses with few components eliciting CPE, whilst the others bees responding to all components (class II) or to none (classes III, IV). These data show that complex odour recognition based on salient components relies on learning abilities.

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DIPLOID ANDRENID MALES CAN BE RECOGNIZED USING MORPHOMETRIC DATA

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In Hymenoptera, fertilized eggs that are homozygous at one or more highly polymorphic sex determining loci develop into diploid males. The frequency of such diploid males in a population depends, among other factors, on the number of loci involved and on the number and frequency of the sex alleles present in a population.

In several taxa of bees a low percentage of aberrant males have been found. These males are mostly unusually large. Leys (1991) has shown that in an isolated population of the communal species *Andrena ferox* two groups of males exist, that can be distinguished on the basis of the length of the distoposterior vein of the second submarginal cell.

Here evidence is presented showing that these unusually large males are diploid. The ploidy was determined by measuring the DNA content of cell nuclei, and of sperm cells using a photospectrometer. The possibility to distinguish haploid from diploid males using morphometric data offers a simple tool to estimate inbreeding coefficients by comparing the frequency of diploid males in field populations. Such knowledge is valuable, not only from an academic point of view, but it can also be very useful in conservation biology.

PATTERNS OF SOCIAL PARASITISM BY AN ALLODAPINE CUCKOO BEE IN DISTINCT POPULATIONS OF ITS ALLODAPINE HOST.

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In montane populations of the Australian allodapine bee *Exoneura bicolor*, newly founded nests are more heavily parasitised by the cuckoo bee *Inquilina schwarzi*, than reused nests. This study examines parasitism rates in both a wet montane habitat and a subcoastal heathland habitat in Victoria, using data collected over several years at each location. The rate of parasitism was found to be much higher in the montane population than it is in the heathland population. Possible reasons for this are the difference in spatial distribution of host nests, or the shorter period of seasonal activity in the montane population. A further finding of the study was that, although the rate of parasitism is higher for newly-founded nests than for nests which were founded in a previous season in the montane population, the situation is reversed in the heathland population. Although this observation could be due to the difference in habitat affecting host and parasite ecology, it supports the hypothesis that variable oviposition rates of hosts throughout the period of seasonal activity affect oviposition strategies of the parasite. This is because, in the montane population, oviposition by females in newly founded nests is highly synchronised by comparison with that of females in re-used nests. In the heathland population, females in re-used nests oviposit with greater synchrony than do females in newly-founded nests. These findings parallel those of Wcislo (1981) that higher synchrony in host life cycles brings about higher parasitism rates.

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MATING BEHAVIOUR IN *BOMBUS TERRESTRIS* L (HYMENOPTERA, APIDAE)

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Male bumblebee behaviour is characterized by the deposition of odorous secretions on certain spots along flight paths. These flight paths may be used by several males. The experiments were carried out in a flight cage of 9x6x3 m placed in the open field, suitable for the males to perform their patrolling behaviour. The study aimed to find out whether these markings are attractive to the queens and enhance the probability of a mating to occur. The possible additive effect of several males marking the same spot on the queen has been investigated.

The results indicate that both queens and males are attracted by male's scent markings. Matings almost always took place at the marked spots. If given a choice between a spot marked by one male and a spot marked by several males, most of the queens choosed the multiple marked spot.

PROTEIN CONTENTS OF VENOM GLANDS IN *Apis mellifera* (HYMENOPTERA, APIDAE) WORKERS OF DIFFERENT AGES AND AT THREE INTERVALS AFTER VENOM EXTRACTION.

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During the Summer period of December 1993 to January 1994, *Apis mellifera* workers of different ages were collected and submitted to electric shock for emptying the venom reservoirs with the purpose of studying the dynamics of the venom replenishment. The total protein content of venom glands of five workers of each age (7,14,21,28,35 and 40 days) was quantified through the modified Bradford's method, before the electrical shocks (control groups) and at regular intervals (24, 48 and 96 hs) after it (experimental groups). Although workers of the experimental groups retake the venom production, in no case the protein level of the control groups is ever reached. The maximum levels of replenishment and the necessary periods to reach them varied within each group and among them. The protein content in the control group was the least at 7 days increasing steadily afterwards and reaching three times that value at 14-28 days. From this age on the protein level was reduced. In relation to this initial levels the following results were obtained in each experimental group at the specific periods after the extraction of the venom: 1. at 7 days, 90% after 48-96 h; 2. at 14 days, 70% after 48 h; 3. at 21 days, 65% after 24 h; 4. at 28 days 50% after 24 h; 5. at 35 and 40 days, 10% after 24,48 and 96 h. We have showed that the potencial capacity of the cells for the venom secretion decrease with age. Beside this the older the workers the faster the maximum level is reached. In absolute values of protein content the middle - aged workers (14 - 28 days) produce the highest protein level in the glandular process of venom replenishment.

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BEHAVIOURAL PROFILES IN LABORATORY COLONIES OF *KALOTERMES FLAVICOLLIS* (ISOPTERA: KALOTERMITIDAE)

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An ethological investigation on members of laboratory colonies of *Kaloterme flavicollis* was performed in order to identify behavioural patterns of different castes and, possibly, to clarify how regulation of social organization takes place in this termite species. Experimental colonies consisting of a couple of replacement reproductives, 1 soldier and 24 members of later developmental stages (either pseudergates or nymphs), were placed in transparent artificial nests and videorecorded for 6 minutes 5 times a day for 7 consecutive days. As event recorder was employed the Observer, an advanced system for collection and analysis of observational data. Data analysis using ANOVA and non-parametrical tests was performed on total duration and frequency of occurrence of each behaviour in every sample period (360 sec) for each focal subject. Significant differences in expression of observed behaviours could be recognized: resting and walking appeared the longest and most frequent behaviour for all castes, pseudergates being the most active (resting accounted for less than 50% of sampled time) and soldiers the most idle (almost 70% of time spent on resting). Only pseudergates and nymphs were observed nibbling (3% of their time). Vibrating and pulsating behaviours were common for all castes, but appeared mostly in nymphs (almost 7% of observed time). Allogrooming bouts were observed among all members of colonies. Soldiers groomed (almost 1% of time) pseudergates or nymphs mostly in the anal region and were groomed (1.7 %) by them in mouthparts and abdomen. Among nymphs, grooming appeared less frequent than among pseudergates, while reproductives spent almost 5% of their time in grooming and appeared to receive it mostly than any other member of the colony (almost 5.3% of observed time) over all body surface. This study appears to confirm the role of pseudergates and nymphs in performing task of feeding all colony members via trophallaxis and suggests that vibratory movements may be used as a mean of communication among individuals (Sbrenna et al., 1992).

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DO QUEEN REMOVAL HAVE ANY EFFECT ON WORKER ACTIVITY IN A PAPER WASP *POLISTES JADWIGAE*?

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Reeve and Gamboa (1983) found that queen removal caused a significant reduction in the average activity level of workers in a North American paper wasp, *Polistes fuscatus*, and hypothesized that the queen was a central pacemaker and coordinator of colony activity. Their hypothesis, however, has not been tested in other paper wasps. I made an experiment of queen removal in a Japanese haplometrotic species, *P. jadvigae*, following a similar procedure to that of Reeve and Gamboa in order to learn how it would affect worker activity levels. The experiment was made in 1993 with four nests that had been transplanted into observation boxes before worker emergence. Observation was made on two consecutive days on each nest which then contained a single foundress and 6 to 12 individually marked workers. On the first of the two days, four one-hour observations were made with intervals of 0.5 hour, and behavior of each wasp was recorded. If a wasp was motionless, or engaged in grooming or fanning, it was considered "inactive", while "active" when it engaged in other behaviors, e.g. feeding or nest construction. On the second day, the queen was removed from the nest after two hours of observation, and another two observations were made on the queenless nest. Mean activity levels of workers before and after the queen removal on the second day were compared for each nest. Results of the first day were used to adjust those of the second day in regard with diurnal fluctuations in activity level. I found no significant reduction in mean activity level of workers after the queen removal in any of the nests. Then, the queen of *P. jadvigae*, unlike that of *P. fuscatus*, does not seem to play a significant role in pacemaking of worker activity levels.

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USE OF FLORAL RESOURCES BY *NANNOTRIGONA TESTACEICORNIS* (APIDAE, MELIPONINAE)

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By means of pollen analysis the botanic species visited for pollen by two colonies of *N. testaceicornis* were identified. Pollen was collected weekly from bee's corbícula along 7 months (Dec/91 to Jun/92). Twice a month pollen samples were also collected from the newer pollen pots. The species more important as food sources in the weekly samples were: *Eucalyptus* spp, *Piptadenia gonoacantha*, *Pyracantha coccinea* and *Schinus terebinthifolius*. For the fortnightly samples the following species were more relevant: *Cedrela fissilis*, *Eucalyptus* spp, *Leucaena leucocephala*, *Piptadenia gonoacantha*, *Schizolobium* sp, *Sthruvantus andrastylus* and an undetermined pollen grain. As it was verified for several species of stingless bees and *Apis mellifera* in the same study site, in autumn and winter (from March to August) *Eucalyptus* spp was one of the most important pollen sources. *N. testaceicornis* had utilized it almost exclusively at this time. In the other months what happens generally is a diversified harvest and a more heterogeneous distribution of bees on available food sources, perhaps by a more diversified offer of pollen and less abundant flowerings. If the two types of sampling (weekly and fortnightly) are compared, the former can be considered as deficient, because it underestimates some species (*P. gonoacantha* and *S. andrastylus*) and overestimates others (*S. terebinthifolius* and *P. coccinea*), being this true only for December and January, for in the other months bees concentrated pollen harvest in a single species, *Eucalyptus* spp.

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EFFECTS OF NOSEMA APIS ON LONGEVITY OF CAGED HONEY BEES (APIS MELLIFERA)**L.A. Malone, H.A. Giacon and M.R. Newton**

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As part of a study to assess the feasibility of breeding honey bees, *Apis mellifera*, resistant to or tolerant of infection with the pathogen, *Nosema apis*, the responses of bees from ten different colonies (headed by queens artificially inseminated with pooled semen from about 200 drones) were assessed. Newly-emerged bees from each colony were dosed individually with 2×10^5 spores of *N. apis*, incubated in cages until death and their longevity and final spore loads determined. The mean longevity of bees from six of the ten colonies was not reduced by dosing with *N. apis* and ranged from 26.5 ± 0.67 days to 38.9 ± 0.64 days, although these bees had higher mean spore loads (137.0 ± 5.63 million spores per bee) than the others (92.1 ± 4.85 million spores per bee). This was not directly attributable to their increased longevity as final spore load was not related to longevity in a linear, logarithmic or square fashion. Additionally, *N. apis* developed at a significantly slower rate in one of the colonies. Bees from a control group from one colony were significantly shorter-lived than those from the other control groups. These data suggest that mechanisms for both resistance to and tolerance of *N. apis* may be operating in New Zealand honey bees and that further investigations are warranted.

PATTERNS OF VOLATILES IN DIFFERENT WORKER DOMINANCE GROUPS OF THE BUMBLEBEE *BOMBUS HYPNORUM* (HYMENOPTERA: APIDAE).

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Among workers of bumblebees sub-castes exist, and a dominance hierarchy is established which is partly connected to the tasks performed by the bees (Röseler & van Honk 1990). In the present investigation on the bumblebee *Bombus hypnorum* we identified and compared patterns of odor compounds of different worker dominance groups.

In a first step the behavior of individual bees was observed to characterize them as dominant, subordinate or foragers. Members of different worker groups showed significantly different behavioral patterns. Dominant workers were more aggressive in interactions with other bees in comparison to subordinate ones and foragers. Furthermore they had significantly larger ovaries than the other bees and tended to have a big fatbody. The odor secretions identified by gaschromatographic analysis in Dufour's gland-, headextracts and cuticular washings as well as headspace samples showed significant differences in both the relative proportions and the total amounts of volatiles. Dominant bees had higher amounts of volatiles than subordinate ones; only low amounts of volatiles could be found in foragers. Whereas dominant and subordinate workers showed very similar patterns of volatiles they differed from foragers and young workers. The identified differences could have a function as pheromonal recognition and dominance signals. Behavioural tests to proof our hypothesis are presently under investigation.

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CYTOGENETIC STUDIES OF NEOTROPICAL SPECIES OF TERMITIDAE (ISOPTERA)

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In order to understand the pathways of chromosomal evolution of Termitidae, 16 Neotropical species were cytogenetically analyzed. Four of them belong to Apicotermitinae, nine to Nasutitermitinae and three to Termitinae. The results with males and females showed diploid number of 42 for both sexes, with one exception - *Neocapritermes opacus* (Termitinae) with $2n=40$ for both male and female. All studied species presented in the first male meiosis a ring or linear chain of 4 chromosomes related to sex, corresponding to a $X_1Y_1X_2Y_2\delta$ - $X_1X_1X_2X_2\phi$ mechanism, originated by reciprocal translocations that involved the primitive Y and an autosome. The primitive Y become a Y_1 , the X a X_1 , the autosome translocated with Y will be the Y_2 and his homologous the X_2 . Etiopic species of the family previously studied showed similarity for both, the diploid number and the sex determination mechanism. This fact permitted to conclude that both, sex mechanism and chromosome number are ancestral characteristics for the family.

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NESTS OF *CORNITERMES* AS STRUCTURAL ELEMENTS OF RAIN FORESTS - FIRST RESULTS

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Cornitermes cf. *ovatus* builds nests of organic matter in the soil, which are topped by conical constructions made of anorganic soil (loam) which are up to ≈ 1.20 m high. Generally, 1-6 holes ("chimneys") connect the lower nest with the atmosphere. There are about 2 living and 22 "dead" nests/ hectare, the latter persisting as a slowly eroding elevated soil structure even after the death of the colony. Dead nests are randomly distributed in the forest. We studied the difference in total soil fauna collected with "ground foto eclectors" (1 m², dug 5-15 cm into soil; Funke 1971) placed over *Cornitermes* nests and in the nearby litter without nest. Four eclector pairs were run simultaneously for a month and then transferred to new locations (16 nests studied from Dec. 93 to March 94). Table 1 (results from the first 2 months = 8 eclector pairs) shows that significantly more Collembola, Hemiptera, and Diptera were caught in eclectors on nests than in the controls. We also registered much more large animals (> 1.5 cm body length), mainly Orthoptera (grasshoppers) and spiders in nests (n=25) than in the controls (4). The eclectors failed to collect large spiders and scorpions as well as tiger beetles (Coleoptera, Cicindelidae) which are reportedly associated with the nests, but these previous results indicate that abandoned termite nests represent a structural element of ecosystems which is used by some other arthropods groups.

Table 1: Individual numbers of arthropods in *Cornitermes ovatus* nests in an Amazonian rain forest (Reserva Ducke, near Manaus, Brazil).

	Collembola	Orthoptera	Hemiptera	Coleopt.	Diptera	Hymenopt.	Arachn.	Others
Month 1 (Dec. 1993/Jan. 1994)								
Nest	414	42	98	3511	3382	779	150	32
Control	310	43	45	3559	2566	343	103	25
Month 2 (Jan./Feb. 1994)								
Nest	389	86	102	1342	2813	311	179	107
Control	158	64	36	895	2094	379	169	60
	sign.	n.s.	sign.	n.s.	sign.	n.s.	n.s.	n.s.

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FORAGING ACTIVITY AND ABUNDANCE OF INSECT POLLINATORS ON BALSAM, IMPATIENS BALSAMINA L.

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Studies were made on the distribution, abundance and foraging activity of insect pollinators visiting balsam, Impatiens balsamina L. plants in Shimla hills of North-west Himalayas. The insect pollinators of balsam bloom comprised 16 species belonging to 4 orders and 9 families. Comparative abundance of insects showed that Indian honeybee, Apis cerana F. and bumble bee, Bombus tunicatus S. were the most frequent visitors on this honey plant resource. Other important pollinators were: Halictus sp., Vespa sp., Altica sp., Musca sp. and Lucilia sp., however, European bee, Apis mellifera L. did not visit this crop at all. Foraging studies revealed that B. tunicatus S. commenced its activity significantly earlier in the morning and also ceased significantly earlier in the evening than A. cerana. Peak period of foraging activity was between 1000-1100h for B. tunicatus and 1100-1200h for A. cerana. There was no significant difference in time spent by A. cerana and B. tunicatus on balsam flowers. Indian hive bee showed diurnal fluctuations in the percentage of pollen, nectar and pollen plus nectar collectors. Other foraging parameters like number of flowers visited per minute, time taken to shift from flower to flower, weight of nectar load, landing and departure patterns etc. have also been discussed. An attempt has been made to study the interaction between foraging activity of honeybees and environmental factors.

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NATURAL HISTORY OF *MICROSTIGMUS NIGROPHTHALMUS* (HYMENOPTERA, SPHECIDAE).

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Among the sphecid wasps, coexistence of females in the same nest has been detected in several species, but a more complex social organization has been reported only for the genus *Microstigmus*. Despite being a diverse and widely distributed group in the Neotropical region, little is known about the biology of *Microstigmus*. Only *M. comes* has been studied in some detail and there is evidence that most of its colonies are eusocial with task division based on size. *Microstigmus nigrophthalmus* is among the biggest species in the genus (length of 5-5.5mm) and its nest is a spherical bag (1.5-2cm in outer diameter) made of small pieces of rotten wood (and other detritus) suspended from a straight petiole (length 12-25mm; mean=16mm). Nest foundation occurs throughout the year, with a peak from January through March. 94% of the nests were founded by a single female (n=65) and in only 5% of the new nests was there any male associated. About 69% of the new nests (n=32) survive the first month, 56% the second month, and only 34% the third month. The larvae are fed progressively with cicadellid nymphs and assume a upside-down position after finishing feeding. The larval feces are removed by the adults and the brood cells remain open during the pupation period. The sex ratio among the first brood of young nests (n=17) was: 1st pupa=1:16 (M:F); 2nd pupa=1:0.9; 3rd pupa=1:4.7; total sex ratio=1:2.9. The mean developmental time (egg to adult) was 77 days (58-125d), and only 27% of the new nests (n=32) produced any offspring. The newly emerged adults, including the males, remain at the maternal nests, but some females seem to leave to found their own nests. The overlap of generations varied from 0 to 86 days (mean=30; n=17). No inhibition of ovarian development among females was detected since only young females had undeveloped ovaries. Also, all females were inseminated, except the very young ones. In the nests with more than one female, it was common to find cells with 2 eggs (sometimes 3), even when there were empty cells available. Some of the observations suggest occurrence of oophagy by females. However the data obtained were not conclusive about the occurrence of dominance and division of labor among females. Several instances of trophallactic behavior were observed among adults (Melo & Campos 1993).

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A QUALITY CONTROL OF COMMERCIAL PROPOLIS BASED ON THEIR ANTIMICROBIAL POTENCY

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A significant number of papers describes propolis by quantitative assays like chromatography. Although such assays detect different compounds of these material, they do not measure if these compounds are active or not. We have been testing the activity of 12 samples of commercial propolis (in ethanolic extract) from São Paulo City (Brazil) against *Staphylococcus aureus*, *Bacillus cereus*, *B. thuringiensis*, *B. subtilis*, *Escherichia coli*, *Pseudomonas aeruginosa*, *Proteus vulgaris*, *P. morgani*, *Enterobacter cloacae*, *Serratia marcescens*, *Yersinia enterocolitica*, *Salmonella cholerae-suis*, *Trichosporon cutaneum*, *Rhodotorula glutinis*, *Candida crusei*, *Geotrichum sp.*, *Candida albicans* and *Cryptococcus laurentii*. The first step of this work was to measure the real concentration of such commercial propolis by dry weigh of solid resinous material. Presence of antimicrobial activity was tested by Disk-Assay System and positive materials were also assayed to Minimal Inhibitory Concentration. We found bacterial strains that were resistant to propolis but sensitive to commercial antibiotics. So it was possible to detect adulterations of propolis carried out by addition of those antibiotics.

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POLYDOMOUS SOCIETIES OF THE TREE-DWELLING ANT *POLYRHACHIS LABORIOSA* (F. SMITH)

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Polyrhachis laboriosa is a sub-dominant, tree-dwelling ant of the African equatorial forest. Its nests are found along the forest edge, in bushes or small (2-10 meters high) trees, under or between the narrowly-spaced leaves of the upper branches. Workers collect vegetal fragments on the ground or in the trees and weave them together with saliva and spider's web. Each nest contains 100 to 1,500 workers, brood and, possibly, alates. A study of the distribution of *Polyrhachis laboriosa* was conducted in a mango grove of the Agronomic Research Institute of Cameroon, near Yaoundé. Preliminary studies conducted by Dejean *et al.* (1994) showed that intraspecific aggressivity in this species is very strong; it permitted to think that grouped nests belong to the same polydomous society. A second study, designed to investigate intraspecific aggressivity, was also conducted both in the laboratory and in the field. Sixty dyadic encounters (5 mn long) were set up between workers collected from the mango grove and belonging to three different nests, one of which was at a distance of 150 meters from the others. Intraspecific aggressivity was non-existent between the two neighbouring nests and very strong between those two and the distant nest. A test of intraspecific aggressivity was conducted in the field in order to control whether or not ants installed on neighbouring trees belong to the same society. Workers taken from two different trees were introduced into a small box. The results of the tests enabled us to determine the territory of each society. *Polyrhachis laboriosa* was thought to be a species which lived in small societies, since each nest was seen as a complete society; however, the two studies showed that *Polyrhachis laboriosa* can live in large, polydomous societies whose nest are distributed among several trees over a surface area of 100 to 3,000 sq. m.; one tree can be occupied by 1-6 nests belonging to the same society.

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CHEMICAL SIGNATURE IN THE ANT *CAMPONOTUS VAGUS* : PERCEPTION AND REGULATION

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In order to investigate the homogeneity of the chemical signature among the members of an ant society, we studied in the ant *Camponotus vagus* the behavioural activities involving a worker topically treated with (Z)-9-tricosene (a hydrocarbon which is not normally synthesized) and 5 untreated workers, and the transfer of this substance with time. It was established in a previous study that in this species, the colony's chemical signature is composed of cuticular hydrocarbons (Bonavita-Cougourdan et al., 1987). The behavioural data obtained show that untreated workers perceived the (Z)-9-tricosene on the cuticle of the treated worker (the number of antennations increased) within the first few minutes of cohabitation and then became habituated to the presence of this substance (the number of antennations decreased). Upon topically applying *n*-tetracosane (an endogenous hydrocarbon existing in traces in this species), it was established that in the cuticular profiles of previously isolated workers, the levels of this hydrocarbon decreased slowly and tended to plateau (50 % of the quantity deposited had disappeared after about 6 days), whereas the levels of topically applied (Z)-9-tricosene decreased dramatically (50 % disappeared at about 6 hrs); the synthesis of *n*-tetracosane was therefore probably enhanced. To investigate the transfer of (Z)-9-tricosene, cuticular extracts of all six workers in each group were analysed after 30, 90 minutes and 9, 24, 48, 96, 168, 264 and 336 hours of cohabitation. The post-pharyngeal glands were dissected out and chemical analysis was performed on groups of ants after the same periods of cohabitation as above: the results show that (Z)-9-tricosene was present in the post-pharyngeal glands from 30 min to 168 hrs of cohabitation, the highest levels being recorded in all six workers in each group at about 24 hours. The GC-MS analyses show that (Z)-9-tricosene was present in the cuticles of some untreated workers only after 96 and 168 hrs of cohabitation. These data show that 1) the (Z)-9-tricosene decreased very quickly on the cuticle of the treated workers, but that the total quantity deposited was spread over the cuticle and post-pharyngeal glands of all the workers in each group at about 24 hrs of cohabitation during licking, grooming and trophallactic activities; 2) it was then reincorporated (1 % of the deposited quantity) into the cuticle of untreated workers within cohabitation periods of 4 and 7 days. Direct contact had to occur between the worker treated with (Z)-9-tricosene and the other workers with which it cohabited for the latter's post-pharyngeal glands and cuticle to show any appreciable amounts of this substance.

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NEST AND SOCIAL BEHAVIOR OF *LIOSTENOGASTER* SP.

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Species of the genus, *Liostenogaster*, are known to build a very variety of nests (Ohgushi et al., 1990; Turillazzi, 1991), but their social life was little known. Five colonies of *Liostenogaster* sp. were collected in Pasoh, Malaysia, and intra-nidal activities of adults in one colony were observed for two hours on 10 Mar. 1993. Nest contents were carefully examined and adults were dissected to inspect the degree of ovarian development and the condition of spermatheca. Nests were built on the underside of the zinc roof of a hut. They lacked an envelope. A side of a cell, which was made of pulp, was directly attached to the substrata. Cells were arranged side by side. Each nest had five to 16 cells and four to ten immatures. All pupae (nine in five nests) were females. Adult population was from one to five. They were all females, and had nearly the same body size. Dominance-subordination behavior was observed 5 times among 3 out of five wasps. The dominant had well developed ovaries, produced abdominal substance, never left the nest, whereas two subordinates had less developed ovaries, left the nest and sometimes returned with nest materials. These three were inseminated. From the above observations, their social life is inferred to be very primitively eusocial.

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COMPARED SPATIAL DISTRIBUTION WITHIN THE NEST
BETWEEN THE ANT SPECIES *CAMPONOTUS PERTHIANA*
(FORMICINAE) AND *PACHYCONDYLA SOROR* (PONERINAE)

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In the socially advanced subfamilies of ants appear more complex behaviours and more tight co-operation between nestmates. This implies more inter individual dependence. As a logical consequence, individuals should stand closer each other inside the nest in advanced subfamilies than in more conservative ones. In fact, a short distance to the nearest neighbour (DDN) should facilitate interactions. In order to test this hypothesis, we compared the distribution within the nest in a *Camponotus perthiana* (more advanced) colony to the distribution within a *Pachycondyla soror* (more primitive) colony. Both distributions were studied for several density situations within the nest. The distance to the nearest neighbour (DNN) and the distance to the centroid (DC) (centre of gravity) were compared between species and for each density. *C. perthiana* was expected to have less variable DNN and DC values than *P. soror*. The comparison between both colonies and a random distribution showed that in both species the distribution of individuals within the nest was not random. The average DNN and DC values were higher and more variable (greater standard deviation) in *P. soror* than in *C. perthiana*, specially for low-density situations. The difference was more marked for DC than for DNN. The higher proximity between *C. perthiana* nestmates (lower DNN) should be correlated with their higher co-operation; and their higher tendency to aggregate (lower DC) should result from the greater queen attractiveness among socially more advanced species.

EVOLUTION BIOLOGIQUE DES INTERACTIONS PLANTES-FOURMIS. RÔLES DES NECTAIRES EXTRA-FLORAUX ET DES CORPS NOURRICIERS

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L'étude des interactions plantes-fourmis est orientée vers la mise en évidence des différents niveaux de spécialisation qui conduisent d'une simple relation de rencontre à une association stricte où plantes et fourmis ont une activité biologique synchrone et où chaque partenaire trouve des avantages essentiels à son développement : nutrition et habitat pour les fourmis, protection et nutrition pour la plante. Dans cette approche nous avons considéré parallèlement les plantes terrestres et les épiphytes, les conditions écologiques de ces deux types biologiques étant différentes. L'étude est menée sur le terrain, principalement en Guyane Française et en serre, en présence et en absence des fourmis. Les rythmes de production des substances consommées par les fourmis sont suivis en relation avec l'activité de ces dernières. Au laboratoire, l'analyse des nectars et des corps nourriciers est réalisée et les structures fonctionnelles mises en évidence. Trois niveaux de spécialisation sont reconnus. Chez les plantes terrestres, à la base, se situent des relations diffuses avec l'intervention des nectaires extra-floraux et d'un grand nombre de fourmis (*Euphorbiaceae*, *Malpighiaceae*, *Mimosaceae*, *Passifloraceae*...). Les nectaires sont externes. Puis des associations stables apparaissent dans lesquelles les nectaires peuvent être internes et où un début de spécialisation morphologique de la plante entraîne le maintien sur cette dernière d'une selon les espèces de fourmis (*Anthocleista-Crematogaster*). Enfin, la présence de structures habitables, domaties caulinaires (*Cordia-Allomerus*) ou domaties foliaires (*Maieta-Pheidole*) associées à des nectaires et (ou) à des corps nourriciers (*Cecropia-Azteca*) conduit à des associations strictes. Chez les épiphytes, on part de relations accidentelles avec la présence occasionnelle de fourmis dans le sol suspendu. Puis, avec les "jardins de fourmis" des associations stables s'organisent. Enfin la différenciation de feuilles en urnes ou d'hypocotyles tubérisés permet des associations strictes. Les différentes études nous amènent à considérer, chez les plantes terrestres, le nectaire extra-floral comme l'élément fondamental tandis que les corps nourriciers présents seulement dans les associations strictes se situent en sommet de l'interaction. Dans le cas de l'association *Cecropia obtusa-Azteca*, la production foliaire est accélérée en présence des fourmis tandis que la protection biotique n'est pas évidente. L'amélioration de la nutrition de la plante prend le pas sur la protection. Dans l'évolution, une protection phénologique peut se substituer à la protection biotique. D'un point de vue global, il est nécessaire, dans un milieu donné, de considérer l'ensemble des plantes à dispositifs sécréteurs et les fourmis en présence ainsi que leur degré de spécialisation associative pour évaluer les conséquences sur les systèmes de défense des plantes.

BIOCHEMICAL PURIFICATION AND MOLECULAR CLONING OF ODORANT-BINDING PROTEINS-LIKE OF THE HONEYBEE *APIS MELLIFERA*

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General odorant-binding proteins (gOBP) and pheromone-binding proteins (PBP) were isolated from various species of Vertebrates (Pelosi et al., 1982) and Insects (Lepidoptera: Vogt et al., 1990; Diptera: Pikielny et al., 1994). These proteins are likely to be involved in solubilization and transport of the lipophilic odorant molecules through the extracellular lymph of olfactory neurons. They could constitute a first step in odor discrimination and play an important role in the olfactory signal transduction. Although these families have no significant sequence similarities among species, it is conceivable that they are structurally analogous representing evolutionary convergence to a domain structure.

In order to study and quantify the specificity of binding between the proteins and their different putative ligands in the bee (i. e.: the queen pheromone, allelochemicals from plants, cuticular hydrocarbon patterns) we isolated putative OBPs by two different and complementary ways:

Biochemical purification from soluble fraction of antennal extracts and molecular cloning of PCR products (probes deduced from highly conserved Lepidopteran sequences).

The microdiversity obtained by molecular cloning and biochemical technics supports the hypothesis of a preliminar information selectivity in odorant peripheral recognition by OBPs.

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THE RELATIONSHIP BETWEEN AGE STRUCTURE AND PRODUCTIVITY IN THE QUEENLESS PONERINE *DIACAMMA* SP.

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Age-polyethism is a general feature in ant society, which has been discussed to raise the colony efficiency. The problem is that optimal allocation ratio of workers to each task is hardly maintained because change in age structure due to workers' eclosion, aging and death affects colony behaviour. However, no study had revealed actual relationships among age structure, behaviour and productivity of the colony. *Diacamma* sp. shows typical age-polyethism. Young workers stay inside the nest caring brood and old workers go outside. I observed daily change in the number of eclosion and death of workers of three *Diacamma* sp. colonies in two years in laboratory. All workers were individually marked. This enabled me to trace change in age structure throughout the observation. Behaviour patterns of all workers of a colony were observed at monthly interval. Number of broods was also counted. Workers eclosed in batch, but their temporal patterns were different in three colonies. Coefficients of variance of numbers of larvae and cocoons were larger than that of eggs. This suggests the reason of batch eclosion exists in brood raising process, not in egg supply. Because of batch eclosion, age structure changed greatly and affected colony behaviour. Multiple linear regression of the number of eclosion on the frequency of each behavioural category was conducted in a colony. Egg caring had positive relationship with number of eclosion, while larva and cocoon caring had no relationship. The difference appeared to be due to the difference in age specificity of each behaviour. While foraging, walking and allogrooming had positive relationship, guarding, being inactive, nest making and regurgitating had negative relationship. Eclosion patterns of other two colonies were predicted from their age structures and compared with observation. They fitted considerably. It is concluded that age structure of the colony is important for productivity although behavioural flexibility, which is considered to compensate skewed age structure, exists in this species. In natural colony, skewed age-structure is expected due to colony fission or predation during colony emigration. Feedback relationship between age structure and productivity is considered to play an important role in life cycle of colony.

FOOD SUPPLY TO COLONIES OF *IRIDOMYRMEX ANCEPS*, TENDING THE AUSTRALIAN LYCAENID BUTTERFLY *JALMENUS EVAGORAS*.

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The caterpillars and pupae of the Australian lycaenid butterfly *Jalmenus evagoras* are constantly tended by ants, the major tending species being *Iridomyrmex* sp. 25 (ANIC, *anceps* group; hereafter referred to as *I. anceps*). A large proportion of foraging workers from a colony of *I. anceps* is involved in tending *J. evagoras* at any one time, representing a loss of ability to forage on other food sources in the same area. To assess the importance of this to an ant colony, a study was carried out in Cloud's Creek, New South Wales, to quantify the number of ants involved in tending *J. evagoras* and in collecting food from other sources. The area occupied by each of seven ant colonies was mapped, and the distribution of trophobionts, together with the number of ants tending them, recorded. In addition to *J. evagoras*, Homoptera belonging to four families (Eurymelidae, Spondylapsinae, Margarodidae and Membracidae) were found tended by *I. anceps*. The flow rates of ants travelling to and from food plants supporting each type of trophobiont were recorded, and ants collected and weighed to determine the harvesting rate from each food source. Finally, the distribution of worker ants at sugar and protein baits laid down on a grid covering the foraging range of each colony was recorded, and related to the position of available food sources. Results of this study showed that the rate of energy return to colonies of *I. anceps* from tending Homoptera was much greater than that from tending *J. evagoras*, although many more ants were involved in tending the lycaenids. Results of the baiting experiment suggest that the qualitative differences between the secretions of lycaenids and the honeydew of the homopterans may be very important to ant colonies, since colonies tending primarily lycaenids foraged preferentially on sugar baits, while those tending primarily homopterans foraged on protein baits. The difference in energetic expenditure and energetic return for *I. anceps* foraging from lycaenids and homopterans strongly suggest some manipulation of ant foraging behaviour by *J. evagoras*.

PREY CAPTURE BY THE CARPENTER ANT *ATOPOMYRMEX*
MOCQUERYSI ANDRE (FORMICINAE-MYRMICINAE)

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The predatory behaviour of the carpenter ant *Atopomyrmex mocquerisi* André was studied in the field. The sequence of acts during two incidents of capture of the green grasshopper *Homocoryphus* sp. 3 to 5mm and 15 to 20mm respectively are compared. These phases succeeded one another: 1- detection by contact; 2- antennation of prey; 3- attack with immobilization of the prey; 4- recruitment of nestmates situated in the vicinity by alarm pheromone, classic recruitment of nestmates situated in the colony by laying a chemical trail; 5- collective seizure and spread-eagling of the prey; 6- cutting up of the prey; 7- transport of pieces. Note that the stinging phase is absent.

The sequence of acts does not vary significantly with the size of the prey. These results are discussed with reference to another arboreal ants species with large colony sizes: *Oecophylla longinoda* for which numerous data are available (see Dejean 1990; 1991). It appears that in both situations group strategy is used with spread-eagling of the prey and absence of venom utilization. The principal difference occurs after the prey is killed. While *O. longinoda* transport entire prey to the nest, *A. mocquerisi* cut it up on the spot, then small piece of prey are transported to the nest.

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FEEDING BEHAVIOUR AND WORKER POLYMORPHISM IN THE CARPENTER ANT *ATOPOMYRMEX MOCQUERYSI* ANDRÉ (FORMICINAE-MYRMICINAE)

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Atopomyrmex mocquerysi André is an African carpenter myrmicine ant that builds large nests in the main branches and trunks of trees whose distal parts then have a tendency to dry out. This arboreal species has very populous societies able to occupy large trees on which they maintain territories in opposition to those of *Oecophylla longinoda* and *Tetramorium aculeatum* and so belong to the "dominant arboreal ants" whose territories are distributed in a mosaic in the forests' canopy (see Leston 1973).

Polymorphism in the worker caste of *A. mocquerysi* is continuous. The existence of three morphological castes (minor, media and major) was shown thanks to biometrical measurement. We found a single intercaste among the workers. The morphology and the colour of workers' head's varied significantly. Minor workers are all black while the major's head is red. The different sub-castes have distinct sets of tasks. Minor workers are mainly sugar-juice collectors; media and major workers act as hunters and defend the nest entrances. Nest guarding is a blocking behaviour such as the one observed in *Colobopsis truncatus* and *Zacryptocerus texanus*. (Hölldobler & Wilson 1990).

During predatory behaviour, foraging is performed by minor workers. When a prey is discovered, nestmates are recruited to capture and transport it to the nest. There is a correspondance between each task and the worker sub-caste that executes it: The scouts are principally minor workers; among the recruits, media and majors subdue the prey which is then cut on the spot principally by major workers. Transport of the pieces of prey is done mainly by both media and major workers, but certain minors can participate.

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SPATIAL MAPPING OF [^3H]-2DG UPTAKE IN RESPONSE TO DIFFERENT ODOURS IN THE WORKER BEE ANTENNAL LOBE

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In the aim of analysing the decoding of behaviourally discriminant stimuli, the [^3H]-2DG mapping technique has been used. In the antennal lobe, first relay station of the afferent olfactory pathway, the arrangement of the glomeruli into populations innervated by different bundles of sensory fibers is supposed to be the support of functional maps corresponding to different scent-induced metabolic activities. Whatever is the nature of the stimulation (queen pheromone, geraniol, pure air), no heavy labelling is seen in any glomerulus, site of the connections between the receptor cell axons and the local and output lobe neurons. The higher 2DG uptake is always located in the periphery of the lobe, and with a lesser intensity in the external part of the coarse neuropile, raising the question of the functional role of these areas in odour processing. In the periphery of the lobe, as in the borders of the glomeruli, the 2DG could be incorporated in the glial cells, as known in the retina of the drone ; glial cells supplying the neurons with metabolic substrate. In the periphery of the lobe, the two sites of the highest 2DG uptake are often ordered in stripes along the antero-posterior axis. The morphofunctional maps obtained with the different odours tested show a number of common areas. The dorsal anterior region is particularly involved in the decoding of the odours.

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CATAGLYPHIS NIGER, THE FIRST CASE OF POLYGYNIN IN THE GENUS CATAGLYPHIS (HYMENOPTERA: FORMICIDAE).

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Species in the genus *Cataglyphis* are considered, like most Formicine ant species, to have strictly monogynous societies. In contrast, field and laboratory observations conducted on *C. niger* (André) indicated that this species is polygynous. Out of the 26 nests collected, only 9 had a single queen and in four the queens were not found; whereas all of the other 13 nests had multiple gynes, up to 7 in one case and even 17 in another case. Laboratory experiments conducted on 4 of these nests containing either 4 or 5 queens ascertained that all gynes lay fertilized eggs. Our direct observations on other polygynous colonies show that a majority of queens lay fertilized eggs which develop into different worker castes. Our recent investigations in the colony with 17 queens or dealate females show that at least 8 of them lay fertilized eggs. It is interesting to note that the number of workers in these highly polygynous ant societies (with 7 or 17 gynes) is not very great. The mean number of workers in these colonies is 851.

However if *C. niger* is the first verified case of polygyny in the *Cataglyphis* genus, our most recent investigations in Spain show that it may not be the only case. In fact, we found more than one dealate female after excavation of a few nests of *C. hispanica* and *C. velox* (Collaboration with A. Tinaut and A. Lenoir). Queen fecundity in these colonies must be verified. The functional significance of these exceptional cases of polygyny in this "evolved" genus is the subject of present investigations.

QUEEN NUMBER AND NESTMATE RECOGNITION IN THE ANT *CATAGLYPHIS NIGER* (HYMENOPTERA: FORMICIDAE)

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In ant species, the closed state of a society as a means of nestmate recognition is very well known. Many authors admit that monogynous societies principally have very closed colonies, whereas polygynous societies are less closed.

We verified this phenomenon through some ethological experiments on *C. niger*. In fact, this species, in contrast to most Formicine ants, is not strictly monogynous. In the field, one can find both monogynous and polygynous colonies. The colonies can contain a single or more queens (up to 7 in one case and even 17 in another case). We introduced workers originating from a polygynous or monogynous colony into an intraspecific monogynous or polygynous one, and vice versa.

The aggressive reactions of resident ants toward the foreigner and the final result of these introductions (adoption or rejection) was verified after 72 hours.

The results of these experiments show that in general monogynous societies are not significantly more closed than polygynous ones. In reality, it is not the monogynous or polygynous state of the colonies which determine the degree of closure of the societies or the level to which aggressive reactions are induced. It is the origin of the foreign worker which determines whether or not it is recognised and, as such, its rejection or adoption into the colony.

BEHAVIOR REPERTOIRE IN QUEEN HONEYBEES WITH QUANTITATIVE ANALYSIS OF MAJOR BEHAVIORS

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Though the honeybee (*Apis mellifera*) is one of the insects studied most intensively, the full range of its behavior has never been completely described. All the behaviors in any species should first be described, if we wish to know the proper function and situation of a particular behavior of interest to us. Nevertheless, the overly numerous and complex behaviors of worker honeybees have prevented us from trying to describe all the behaviors. As a first step in a trial, I began to study queen behavior. Based on observations of 6 virgin queens and 8 mated queens by the 'single-individual trailing' method (one of the focal-animal sampling methods) for ca. 450 hrs, 46 behavior patterns are described, together with 32 worker behaviors closely related to queens. 'Egg laying', 'royal court formation' and 'balling behavior' are particularly discussed. The latter 2 behaviors, which are worker behaviors and comprise 13 and 12 patterns respectively, may be based on 2 drives, fleeing and aggression. Quantitative analysis of some major behaviors clearly shows behavioral differences between virgin and mated queens. After the start of egg laying, a mated queen becomes the center of her colony and maintains stable interaction between herself and the workers, unlike a virgin queen, which has more workerlike character and is more individual until her mating flight.

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THE RECRUITMENT PHEROMONES OF *APHAENOGASTER* (=NOVOMESSOR) *COCKERELLI* AND *A.* (=NOVOMESSOR) *ALBISETOSUS*, TWO CLOSELY RELATED MYRMICINE ANTS

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Aphaenogaster (=Novomessor) *cockerelli* and *A.* (=Novomessor) *albisetosus*, two closely related ant species, are common in the South-western United States and Northern Mexico. Both species employ a similar, highly effective foraging strategy where workers forage individually, but recruit nest mates to large prey items using chemical (Hölldobler et al. 1978) and vibrational signals (Markl and Hölldobler 1978). Foragers encountering prey, which they are unable to transport back to the nest alone, discharge the contents of their poison glands into the air to attract other workers foraging in the vicinity. If an insufficient number of nest mates are recruited, the scout lays a trail, with the poison gland secretion, from the prey to the nest entrance which stimulates 20-30 workers to leave the nest and follow the trail to the prey. (Hölldobler et al. 1978). We have demonstrated that the poison gland secretion of *A. cockerelli* contains, essentially, a mixture of (R)-1-phenylethanol (87.8 %) and (S)-4-methyl-3-heptanone (10.4 %), while the poison gland secretion of *A. albisetosus* is dominated by a mixture of (S)- and (R)-4-methyl-3-heptanone in the ratio 8:2. Synthetic (R)-1-phenylethanol mimics the activity of the poison gland secretion of *A. cockerelli* completely, even at amounts equivalent to 1/100th of a gland, while (±)-4-methyl-3-heptanone induces no response. Conversely, *A. albisetosus* respond to (±)-4-methyl-3-heptanone, but not to 1-phenylethanol. It has been shown that *A. albisetosus* workers follow the trail pheromone of *A. cockerelli*, but *A. cockerelli* workers do not follow trails laid by *A. albisetosus* (Hölldobler et al. 1978). It is clear from these results that *A. albisetosus* respond to the 4-methyl-3-heptanone component present in the poison gland secretion of *A. cockerelli*.

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FOOD-PROCESSING STRATEGY OF BUMBLEBEES (HYMENOPTERA: APIDAE)

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Social bees forage large amounts of pollen and nectar from flowers. These unstable food resources are their sole nutrition. In the European honeybee (*Apis mellifera*), data on food-storage mechanism such as nectar concentration, sugar inversion by enzymes, and production of gluconic acid and hydrogen peroxide from glucose by glucose oxidase have already been published. However, there are no such data on bumblebees (*Bombus* spp.). This paper discusses the food processing of Japanese bumblebees provided with 40% sucrose solution as a source of carbohydrate in laboratory conditions. Fine powdered pollen was also provided as a source of protein and lipids. The stored honey collected from the honey pot was analyzed. The sugar concentration was ca. 83% and the pH was 3.5. No sucrose was detected but fructose and glucose were identified at a ratio of 8:2. This sugar inversion occurred *in vitro* when a hypopharyngeal gland homogenate was mixed with the substrate. Several organic acids such as acetic acid and lactic acid were identified as minor components. Although hydrogen peroxide was detected in the honey, the major acid was not gluconic acid. Bumblebees produce at least three exocrine enzymes that invert sucrose in nectar and induce antibacterial functions. The pollen was mixed with the stable honey and packed into the pot. This chain reaction enables long-term storage of food. The food processing strategy must have developed in parallel with the evolution of bumblebee eusociality.

ROLE DES TERMITIERES DANS LA DYNAMIQUE D'UNE BROUSSE TIGREE SOUDANO-SAHELIENNE

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La brousse tigrée est une formation végétale particulière qui se rencontre sous une pluviométrie faible, de l'ordre de 600 mm annuels, en Afrique, en Amérique centrale et en Arabie Séoudite. Elle se caractérise par une alternance de bandes boisées et de bandes nues sans végétation. Diverses hypothèses ont été avancées pour expliquer l'origine de cette structure, qui présenterait un déplacement progressif des bandes de végétation vers l'amont de la pente. Le but de notre travail est de caractériser l'hétérogénéité créée par les nids épigés de termites (essentiellement *Macrotermes subhyalinus*) sur la distribution des sols et la végétation et les conséquences de ces interactions dans la dynamique du faciès de brousse tigrée. L'étude est réalisée au nord Yatenga (Burkina Faso). L'abondance des termitières de *Macrotermes*, en activité ou à différents stades d'érosion, varie de 20 à 160/ha, selon la toposéquence. Les nids vivants ont une densité moyenne de 8,4/ha sur l'ensemble des biotopes, mais ne se trouvent, en fait, qu'au sein de l'arc de végétation, où leur densité atteint 21,1/ha. L'échantillonnage des ligneux, sur termitières par rapport au milieu environnant, montre une augmentation des densités de toutes les espèces (224,8 individus/1 000 m² de milieu, au lieu de 130,3). Certaines espèces apparaissent inféodées aux termitières, telle *Boscia senegalensis* (71,2 pieds/1 000 m² sur termitière, contre 6,4) ou *Grewia bicolor* (8,9/1 000 m², contre 0,2 seulement hors termitière). Le milieu "termitière", qui représente 2,5% de la surface au sol, supporte 57% des populations de *Grewia bicolor*, 22,2% de celles de *Boscia senegalensis*, 9,1% de celles d'*Acacia ataxacantha* et 6,5% de celles de *Pterocarpus lucens*. Ainsi qu'il a été dit, les termitières vivantes actuelles se localisent à l'intérieur de l'arc de végétation. La distribution des stades d'érosion montrent que les stades les plus érodés, donc les plus anciens, se rencontrent dans la bande nue. Les termitières de *Macrotermes subhyalinus* répondent, comme la végétation, aux variations du régime hydrique qui expliquent la dynamique de la brousse tigrée, avec une alimentation correcte en amont des bandes de végétation et une alimentation déficitaire en aval. Toutefois, l'action des termites se superpose à cette dynamique en l'accentuant. Dans les fourrés, les nids vivants contribuent, par leurs activités de récolte et de remaniement du sol, à favoriser l'infiltration. Dans les bandes nues, les nids morts offrent une prise à l'érosion de leurs éléments fins et accroissent ainsi les phénomènes de battance, par formation de croûtes d'érosion.

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OOSORPTION AND SPERMATHECAL MORPHOLOGY IN THREE SPECIES OF WILD BEES

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The reproductive division of labour that characterizes eusociality ultimately has a physiological explanation. Although many halictine workers have well developed ovaries, the genetic data suggests they rarely produce offspring successfully (Packer, 1994, *Behav. Ecol. Sociobiol.* vol.33, no.1) and the eggs that they develop are either resorbed or eaten by nestmates after being laid (Packer, 1986, unpubl. Ph.D. thesis).

Eusocial species lay more eggs than solitary species, consequently, differences in sperm utilization between these two groups may be expected to generate differences in spermathecal morphology and physiology.

Ovarian development and resorption and spermathecal morphology in three species of bees representing solitary (*Megachile relativa*), semisocial (*Lasioglossum comagenense*), and primitively eusocial (*Halictus ligatus*) behaviour patterns were compared. Few hundred bees of each of the three species were caught. Some were immediately placed in buffered formalin (0h) and the rest were individually kept captive at 4°C for up to 50h. The bees were then pickled after each 10h interval. Standard histological protocol for whole-mount ovaries was followed, carbol-thionine staining was done according to Goukon *et al.* (1987, *Res. Popul. Ecol.* vol. 29, no. 2).

Preliminary data seem to show that oocytes in the oviposition stage (degenerating from post-vitellogenic eggs) are preferentially resorbed over eggs in the non-oviposition period. Data already available on spermathecal morphology indicate that the primitively eusocial species has a spermathecal chamber with greater dimensions which suggests that it may accommodate more sperm. A larger spermathecal gland in the social species suggests the possible modulation of its secretory function relative to a larger chamber. These studies will be extended to solitary and primitively eusocial and also cleptoparasitic species in the future.

SPATIAL SEQUENTIAL MEMORY IN THE ANT *CATAGLYPHIS CURSOR*

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Worker ants of the species *Cataglyphis cursor* individually forage using terrestrial visual cues. Former laboratory experiments indicated that *C. cursor* can encode and store both the compasses and the spatial relationships of different visual landmarks, which were present in the same time on a circular visual panorama, in order to accurately locate the direction of their nest (Pastergue et al., 1992). We tested in the present work how *C. cursor* ants can manage to find their way back home when constrained to route following. Four sequentially separated rooms (A, B, C, D), connected with plastic tubes, linked a food site to the nest. In each room, ants were confronted with a spatial binary choice corresponding to the entry of one of two plastic tubes, one leading to a dead-end ("wrong" choice) and the other one to the following room ("correct" choice), and this up to the nest entry. Each of the two issues in each room was identified by a specific visual landmark, i.e. a cross (indicating the correct entry) versus a circle (indicating the wrong entry) or a triangle versus a square, and so on. The daily position of the correct issue, be it on the right or on the left side of the wrong issue, was alternately changed in each room to prevent ants using idiothetic information. Ants rapidly learned the correct sequence of visual cues and homed rapidly. If visual information in one of the four rooms was missing, ants were somewhat disturbed but nevertheless homed correctly. This clearly indicates that the sequential spatial memory of the workers can be used in a flexible way, allowing ants to go directly from A to C. However, when the first landmark, corresponding to the first correct choice leading from site A to site B, was presented in a binary choice as against the second (leading from B to C) or the third landmark (from C to D), ants preferentially chose the first landmark. This shows that ants are correctly expecting the first learned landmark to be located at the first site at the beginning of the homing path. In contrast, whatever the stage of the spatial sequence, i.e. in room A, B or C, ants have more difficulty to choose the expected correct landmark in the corresponding room when it is presented as against the last correct landmark, i.e. the one indicating the tube leading from site D to the nest. Thus, ants seem to not allot the same weight to each of the memorized landmarks as a function of its local position in the sequence.

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PTTH-immunoreactive neurons in the central nervous system of the honey bee, *Apis mellifera*.

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In last instar honey bee larvae, the ecdysteroid-producing prothoracic gland (PG) shows caste-specific patterns of activity (Hartfelder, 1993). Since in many insects PG activity is controlled by prothoracicotrophic hormone (PTTH), a brain neuropeptide, we mapped PTTH-immunoreactive neurons in the honey bee larval brain. Brains were dissected and fixed in Bouin's solution at 4°C. PTTH neurons were identified in whole mounts and in paraffin sections by incubation with a polyclonal rabbit antibody (diluted 1:200) directed against the N-terminal amino acid sequence of *Bombyx mori* PTTH (Mizoguchi et al., 1990). Immunoreactive neurons were revealed by a peroxidase-conjugated secondary antibody or a peroxidase-anti-peroxidase system. In brains of spinning-phase larvae, 5 groups of neurons showed PTTH immunoreactivity in a bilaterally symmetric arrangement in each brain hemisphere. 3 groups are situated in the protocerebrum around the optic lobes: cluster 1, a single neuron is mid dorsal of the lamina; cluster 2, a group of 3 neurons lies dorsally between lamina and medulla; cluster 3, consisting of 2 neurons is located at the lateral margin of the optic lobe. 2 deutocerebral PTTH-immunoreactive neurons were found near the antennal lobes, and 2 large neurons were localized in the tritocerebrum surrounding the oesophageal passage. During metamorphosis this cellular pattern changed. In early pupal stages, only one neuron, a large neuron in the pars intercerebralis of the protocerebrum in each hemisphere, continued to express the PTTH-like peptide phenotype. For the first time in development we could also observe immunoreactive material in some of the pupal axons. PTTH-immunoreactive neurons were also found in the ventral ganglia of these early pupal stages with one neuron per hemineuromere. The identification of neurons producing a PTTH-like peptide in the honey bee brain and ventral nerve cord contributes to our understanding of the organization of a neuroendocrine axis which regulates metamorphosis and caste development in *Apis mellifera*.

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Serotonin-immunoreactive neurons in the central nervous system of honey bee (*Apis mellifera*) larvae

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Serotonin (5-HT) is a potent stimulator of in vitro juvenile hormone synthesis in honey bee larvae (Rachinsky, 1994). To understand its significance in honey bee caste development we mapped the serotonin-immunoreactive (5-HTi) neurons in the CNS of larval honey bees. Brains and ventral nerve cords were dissected from fifth instar queen and worker larvae and were fixed in paraformaldehyde/picric acid solution. Immunocytochemistry was performed on whole mounts and on paraffin sections using a well-characterized anti-5HT antiserum (Granger et al. 1989). Visualization of 5-HTi neurons was by PAP reaction. 18-20 somata were visible in each brain hemisphere. The 15 protocerebral neurons were grouped into 4 clusters: Cluster 1, 7 neuronal somata is located in a dorso-median position between the lamina and the neurilemma; cluster 2, a single neuron in a dorso-frontal position; cluster 3, 3-5 neurons in the pars intercerebralis; cluster 4, 2 neurons situated laterally, between the lamina and the neurilemma in the optic lobe. In the deutocerebrum 2 immunoreactive neurons were found in the antennal lobe, and 3 neurons were identified in the tritocerebrum. Only somata but no 5-HTi axons could be revealed in the larval brains. In the ventral nerve cord (VNC), 56 immunoreactive cell bodies, axons, and fine processes were clearly discernible. Organization of the serotonergic system in the VNC is bilaterally symmetric. A pair of 5-HTi somata is located in the latero-caudal part of each hemiganglion. Each neuron sends its axon contralaterally via a ventral commissure. Both axons then project anteriorly, one of them terminating in the caudal neuropil of the next hemiganglion, and the other one traversing several of the anterior neuromeres. Dendritic processes with abundant varicosities are in close proximity of the somata. Most of these 5-HTi neurons in the VNC were found to persist during metamorphosis. As no brain 5-HTi axons could be found to descend to the corpora allata it is difficult to consider a physiological role for serotonin in regulating JH synthesis. The only possibility would be a serotonin release from the varicosities in the VNC ganglia.

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UPDATE ON THE ERGATOID QUEEN/INTERCASTE CONTROVERSY IN ANTS

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The characteristics of caste dimorphism vary considerably in ants. With the notable exception of ponerine species with gamergates, individuals who reproduce are phenotypically distinct from the worker caste. In a minority of species however, the reproductives are permanently wingless, although their thorax is unlike that of workers. Peeters (1991) emphasized that ergatoid queens and intercastes represent two different morphological categories. The latter exhibit various combinations of queen and worker characters, and seem to be produced by a developmental pathway which is distinct from that of the queen caste. In various species they may have a reproductive function, and can replace the queens. In contrast, ergatoid queens are often highly specialized for egg production, although they have lost the ability to disperse by flight. In order to differentiate between ergatoid queens and intercastes, it is necessary to compare both their functional characteristics and their morphological differences.

As wingless reproductives are studied in more species, the concept of intercastes needs to be refined. Recent published data on *Technomyrmex albipes*, *Ephebomyrmex imberbicus* and *Myrmecina graminicola* will be reviewed for this purpose.

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Tsuji, K., T. Furukawa, K. Kinomura, H. Takamine and K. Yamauchi, 1991. The caste system of the dolichoderine ant *Technomyrmex albipes* (Hymenoptera: Formicidae): morphological description of queens, workers and reproductively active intercastes. Ins. Soc. 38: 413-422.

HYDROCARBON BIOSYNTHESIS IN ARTIFICIAL MIXED-SPECIES GROUPS OF ANTS

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Social insects maintain a closed society that excludes all but their own conspecific colony members. Cuticular hydrocarbons are a major part of the chemical signature by which nestmates are recognized: they are both species- and colony-specific discriminators. Errard and Jallon (1987) described the convergence of hydrocarbon patterns between two ant species, *Manica rubida* and *Formica selysi* (Hymenoptera, Formicidae), after they had been reared in mixed-species groups. The new chemical signature resulted in qualitative and quantitative changes of hydrocarbons in each species which probably allowed them to cohabit and display cooperative behavior. When reared in mixed-species groups, *M. rubida* hydrocarbons showed unsaturated hydrocarbons characteristic of *F. selysi*. Our aim was to understand how the two species acquire new cuticular hydrocarbons (Bagnères *et al.*, 1991). They may exchange cuticular hydrocarbons passively, they may exchange specific precursors involved in hydrocarbon biosynthesis, or new enzymatic steps in the biosynthetic pathway may be activated. These three hypotheses may be complementary.

As hydrocarbons result from fatty acid decarboxylation, their *de novo* biosynthesis was studied after incorporation of labeled free fatty acids (myristic, palmitic and stearic acids) for single-species and mixed-species groups. Experiments were conducted with ants aged 1-6 days, 3 months and 6 months. The results clearly show the ability of the two ant species to synthesize *de novo* cuticular hydrocarbons, independently of age, time of incubation and fatty acid precursors. *M. rubida* produced the unsaturated hydrocarbons characteristic of *F. selysi*. Thus ants can synthesize foreign hydrocarbons by a synthetic pathway activated by the early presence of allospecific social partners and/or by the presence of certain precursors.

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LARVAL FOOD PROCESSING BY ADULT BUMBLEBEE WORKERS

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Bumblebee larvae are fed by workers through progressive feeding. In literature the larval food in *Bombus* is believed to be solely composed of pollen and nectar or honey (Sladen, 1912; Katayama, 1973; Michener, 1974).

Larval food processing and feeding was studied in the bumblebee *Bombus terrestris* by comparing protein contents in samples taken from larval food and crop-contents of the feeding workers. A substantial amount of the proteins present in larval food originates from sources other than from pollen-contents. The free protein concentration of the nectar-pollen mixture in the crop was found to be equal to the protein concentration of larval food immediately after regurgitation. Crop contents of workers feeding on nectar only, merely contain a small amount of free proteins.

It seems probable therefore, that secretions from the hypopharyngeal glands are added during the ingestion of pollen prior to the regurgitation of larval food.

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ANT COMMUNITIES IN DEGRADED FORESTS OF THE KARKONOSZE MOUNTAINS

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Ants are one the components of a complex study of biocenoses undergoing changes as a result of the dying of spruce forests in the Karkonosze Mountains. The study was carried out at many points of a mountain chain with different site conditions, plant communities, and stages of changes in these communities. The richest ant communities /numbers of species, nest density and frequency/ occurred in degraded forests and in ecotone communities at the timber line. Colonization of these habitats by ants depends on the slope /negatively/ and on the degree of tree stand destruction /positively/. The number of ant species and the density of their nests increased along the gradient of habitats situated on the same slope and characterized by different stages of forest degradation and succession of grassy vegetation. The dominant species of *Myrmica* did not differ in the society size in the same habitat. In the successional gradient of the vegetation, the average size of a *Myrmica* society increased, also production and mean weight of workers increased, whereas the biomass turnover of the society decreased. Consumption by ants that is, their impact on other invertebrates increased. This provides evidence for an increasing role of ants in post-forest biocenotic systems of the Karkonosze. Ant communities in these systems become similar to those occurring on mountain meadows.

SOME REMARKS ON THE BIOLOGY OF *CATAGLYPHIS AENESCENS* (NYL.) (HYMENOPTERA, FORMICIDAE).

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Investigations have been carried out in Deliblatska pescara (Deliblato Sandy Area) (Serbia), about 70 km northeast from Belgrade. Up till now, *C. aenescens* has been registered in Federal Republic of Yugoslavia in Deliblatska pescara only. The society of *C. aenescens* consists of several hundreds, up to 2,000-2,500 workers. This species inhabits semidesert habitats. The nest is constructed of a smaller above ground part, like a bulwark, and a bigger subterranean one. The subterranean part is presented by one subsurface part, constructed of passages and chambers in a diameter of about 50-60 cm, and a profounding part, which is presented by one vertical passage, about 1 cm wide and 30-40 cm, up to 1 m long. It usually ends with one chamber. Chambers around it are, more or less, spirally arranged, and it prevents pulling down of one chamber over another, and shows an adaptation to loose soil (sand). The activity of the society begins in spring (March, April), and the maximum is reached in July and August. Each worker begins its activity half an hour to one hour after the sunrise, at the temperature of sand of about 20°C, and the maximum is reached at the hottest period of the day, when the temperature of sand can reach 50-60°C. *C. aenescens* is a chiefly diurnal scavenger, foraging on dead arthropods (mostly insects). Plant material and plant saps account for smaller portion of dietary resources of *C. aenescens*. It is overwintering in adult stage. During the winter and early spring, at the depth of 70-80 cm, and the temperature of 7-8°C, in 2-3 chambers, clusters of workers, together with queen were found. It should be pointed out, that *C. aenescens*, belonging to the group of "desert ants", has a significant role in poor semidesert and desert habitats of Deliblatska pescara.

SURVIVAL OF HONEYBEES (*APIS MELLIFERA* POLLM.) AFTER DRIFTING INTO RELATED OR NON-RELATED COLONIES

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Drifting of honeybees is influenced by many parameters, such as height and color of the hives, their spatial separation and arrangement, as well as landmarks nearby the apiary (Frisch, 1977; Jay, 1966). Recent research has demonstrated that honeybees are able to recognize related and non-related individuals (Page et al., 1991). To determine whether genetical factors influence drifting, twelve artificial swarms were established and introduced into two linear apiaries consisting of 8 and 4 hives. The colonies alternately received sister queens of two non-related genetic lines. The hives of the apiary had no unique visual marks. From each colony 200 newly emerged bees were marked individually. Half of these were reintroduced to their colony of origin (native-bees) and half to an adjacent non-related colony (foreign-bees). The colonies were examined 2, 6, 9, 16, 25 and 34 days later for the presence and identity of all marked bees. There was no difference in the acceptance of native- and foreign-bees by the colonies. On the second day 98% of both groups were found to have been accepted. Drifting of native- and foreign-bees was unexpectedly high. During the experiment on average of 75% of all marked bees from both genetic lines drifted at least once among the interior colonies of the apiary. Drifting from the outer colonies was significantly lower (about 19%). There was no tendency to prefer related colonies when drifting. As a result of the high level of drifting we calculated that 36% of bees in an interior colony were not descended from that colony's queen. Native- and foreign-bees of both genetic lineages had the same life expectancy. Similarly life expectancy of drifted bees was not shorter than that of non-drifted bees. The results indicate a high intermix of the population of an apiary when hives are of similar appearance. The fact that drifting did not shorten the lifetime of bees suggests that drifted bees were seldomly attacked by guard bees and were at least tolerated by the native members of a colony.

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INCIDENCES DE CERTAINS PARASITES CHEZ LES BOURDONS

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Dans le milieu naturel, le parasitisme constitue l'un des facteurs limitatifs au développement des colonies de Bourdons. L'élevage contrôlé de reines et de colonies au laboratoire peut favoriser l'apparition de maladies parasitaires, du fait de la concentration des insectes dans un volume restreint où règnent des conditions thermiques et hygrométriques élevées. Notre objectif est d'étudier l'état d'affaiblissement ou les effets létaux provoqués par certaines atteintes parasitaires chez les Bourdons. Les observations ont porté sur des ouvrières, des mâles et des reines de différentes espèces, capturés dans la nature, et sur des individus provenant d'un élevage contrôlé au laboratoire. Dans le cas de maladies parasitaires, nos examens prennent en compte l'identification du germe infectieux, la contamination des insectes en fonction de l'espèce, du sexe, de la caste, et de la force de la colonie, enfin le siège des lésions. Le diagnostic expérimental repose sur des examens macroscopiques d'organes à l'état frais ou des examens sur frottis.

THE SENSORY HAIRS ON THE ANTENNAE OF WORKERS OF THE LEAF-CUTTING ANT *ATTA SEXDENS RUBROPILOSA*.

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Antennae of different castes of *Atta sexdens rubropilosa* workers were examined using scanning electron microscopy. Eight morphologically distinct types of sensory hair could be distinguished, including *sensilla basiconica* (3 types), *s. tichodea* (2 types), *s. chaetica* (2 types) and *s. placodea*. The distribution pattern of each type varied over the length of the antennae and over each segment. Only *s. trichodea* were found on all segments. One type of *s. basiconicum* was always found associated with a hooked type of *s. chaeticum*. The highest density of hairs and the greatest diversity of types occurred at the tip of the antennae. Both density and the number of types decreased towards the scape. Larger workers had a lower density of *sensilla* per unit area but the average size of the hairs was larger. The distribution patterns of the hair types did not vary with worker size.

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**REGULATION OF THE TIMING OF COMB
CONSTRUCTION BY HONEY BEE COLONIES**

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A central goal of insect sociobiology is to understand the mechanisms by which coordinated colony-level actions emerge from the separate behaviors of relatively independent individuals. This study initiates a detailed study of one example of this phenomenon: a honey bee colony's regulation of the timing and amount of its comb construction. Colonies are expected to regulate construction in order to avoid either making too much comb (and thus wasting energy on unnecessary wax production) or making too little (and thus reducing the amount of nectar which can be stored for overwinter survival). I tested the hypothesis that colonies optimize timing by building only when two conditions are satisfied: 1) a nectar flow is in progress, and 2) the amount of empty comb available in the hive has fallen below a threshold value. By working with colonies confined to flight cages, I obtained complete control of the timing and size of nectar flows. I controlled the amount of empty comb in the nest by periodically replacing combs that were too full or too empty with others at the desired degree of fullness. Colonies did not build over a four day period when they had both high nectar intake and a large quantity of empty comb (>90% of cells in storage area of hive were empty). When the bees were allowed to fill up the empty comb, construction began once the proportion of empty cells fell below 60%. Similarly, colonies with little empty comb did not build while nectar intake was very low, but began to build once nectar flow was increased. These results are consistent with the behavior of an unmanipulated colony which initiated construction only when nectar flows coincided with periods of limited empty storage comb within the hive. Further studies during the summer of 1994 will attempt to determine 1) the age caste of the building bees and their behavioral repertory when not building, and 2) the proximate cues used by these bees to monitor the size of nectar intake and the amount of empty comb available.

EXPERIMENTALLY INDUCED DIGYNY IN USUALLY MONOGYNOUS *POLISTES GALLICUS* WASP COLONIES**M. PRATTE and J. GERVET***CNRS - URA Ethologie et Psychologie Animale, Université Paul Sabatier, Toulouse*

The polygynous social and reproductive behaviour of two *Polistes* species, the usually monogynous *P. gallicus* and the potentially polygynous *P. dominulus*, was analysed. In both species, an encounter between two reproductive females led to a fight ending in either the flight or the submission of one of the two wasps and then in the establishment of a digynous colony (primary polygyny, or foundation polygyny). Encounters on a well developed nest led to violent fighting in *P. gallicus*, sometimes ending in death or mutilation. Establishing secondary polygyny was almost impossible in this species. The relationships between associated foundresses were clearly of the dominance / subordination type in both species. Some behavioural differentiation accompanied the hierarchical organization. However, subordinate wasps of *P. gallicus* were able to perform both dominance behaviour and oophagy, which usually occur in the dominant individuals. This refusal of the subordinate role sometimes led to the decline of the brood, and to that of the colony itself. When placed in a polygynous situation, a monogynous species such as *P. gallicus* shows behaviour which is intermediate between strictly territoriality and a truly polygynous behaviour. This intermediate behaviour cannot be said to be an evolutionarily stable strategy because it is accompanied by reciprocal, lasting differential oophagy that result in a decrease in the descendent production.

TAXONOMIC STRUCTURE, DISTRIBUTION AND SPECIES DIVERSITY CENTRES OF THE ANT GENUS *MYRMICA* LATR. IN THE EURASIA

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Myrmica species are the most common ants in the temperate humid Holarctic zones Holarctic. Some of them inhabit steppe and even semi-desert areas; several species are found in the mountain forests of the Oriental region (up to Northern Burma). More than 70 species and about 20 infraspecific forms are known from Eurasia. I established eight species groups of Eurasian *Myrmica*: I. *arnoldii* (2 species); II. *lobicornis* (18); III. *luteola* (1); IV. *ritae* (5); V. *rubra* (11); VI. *rugosa* (7); VII. *scabrinodis* (16) and VIII. *schencki* (4). There are also 9 socially parasitic species probably belonging to the same groups as their hosts. About a half of *Myrmica* species are the most abundant in the following regions and natural zones: 1. Boreal zone - *arnoldii*, *tschekanovskii* (Ist species group), *angulinodis*, *bicolor*, *commarginata*, *forcipata*, *incurvata*, *kamtschatica*, *lobicornis*, *ranssibirica*, *ulcinodis* (II), *rubra*, *ruginodis* (V); 2. European deciduous and mixed forests - *hellenica*, *gallienii*, *rugulosa*, *sabuleti*, *cabrinodis*, *specioides*, *vandeli* (VII) and six socially parasitic species; 3. Steppe and forest-steppe - *kasczenkoi*, *pisarskii*, *zozae* (II), *bergi*, *slovaca*, *stangeana* (VII), *lacustris*, *schencki* (VIII); 4. Hemixerophilous Mediterranean and Caucasian forests - *aloba*, *bessarabica*, *turcica* (VII), *caucasicola*, *ravasinii* (VIII); 5. Mountain forests and meadows of Central Asia - *kirgisorum*, *saposhnikovii* (II), *chinensis*, *dicaporiacoi*, *dshungarica*, *everesti*, *ferganensis*, *juglandeti*, *kryzhanovskii*, *smythiesi*, *tibetana* (V), *helleri*, *inezae*, *kozlovi*, *pachei*, *rugosa*, *specularis* (VI), *aimonis-sabaudiae*, *orthostyla*, *tenuispina* (VII) and one socially parasitic species; 6. Ussurian forests - *aspera*, *carinata*, *excelsa*, *jessensis* (II), *luteola* (III), *kurokii* (VI); 7. Subtropical and tropical mountain forests - *formosae*, *indica*, *margaritae*, *ritae*, *serica* (IV). Based on the distribution and ecological data for *Myrmica* species I distinguish six species diversity centres which presumably are the regions of the origin and evolution of different species groups: Euro-Caucasian (*scabrinodis* and *schencki* groups); East-Siberian (boreal species of *lobicornis* group); South-Siberian and Mongolian (xerophilous species of *lobicornis* group); Ussurian (*luteola* and some specialized species of *lobicornis* group); Central-Asian mountain (*rubra* and *rugosa* groups); South-Asian (*ritae* group). Species of *ritae*-group are the most morphologically primitive and similar to the eocene *M. longispinosa* Mayr. I propose the following evolutionary paths of *Myrmica* species groups: *ritae* *rugosa* *rubra* *lobicornis*, *scabrinodis*, *schencki*.

EUSOCIALITY IN BEES: THE SELECTIVE MECHANISM AND PREREQUISITES MAKING ITS ORIGIN POSSIBLE

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Eusociality does not appear if Hamilton's parameter K (the ratio of genetic relatedness of gyne with own offspring to her genetic relatedness with the reproductive offspring reared in the colony) is equal to or more than one. This law does not depend on the type of organism reproduction and the type of sex determination. Therefore the polygynous family hypothesis as well as the mutualism hypothesis and the parental manipulation hypothesis are based on unrealizable initial conditions. Among other hypotheses only the haplodiploidy hypothesis offers a reasonable explanation of the genetic mechanism for appearance of a sterile caste. Haplodiploidy by itself is not the cause for origin of eusociality at Hymenoptera. However, it ensures the kin selection under some favorable conditions. The cases of polygynous foundation of a colony among primitive eusocial species are often put forward as the main argument against the haplodiploidy hypothesis. We prove that these cases actually are well explained and even are predicted by the haplodiploidy hypothesis. As a rule, polygynous colonies are founded by sisters. Usually only one of them becomes egg layer. Such colonies always develop into ordinary matrilineal communities. Therefore the calculation of the genetic gain of a sister that performs worker functions in a polygynously founded colony should be made for the time period of the whole cycle of colony development. The reproductive offspring of a polygynously founded colony consists of nephews and nieces of this sister (its mean genetical relatedness to them is equal to $3/8$). In a solitary species the offspring for the same period will consist of grandsons and granddaughters of the spring female (her genetic relatedness to them is equal to only $1/4$). Polygynous colony foundation is supported by kin selection, but it occurs only after arise of eusociality. The original sense of the term «subsociability» proposed by Wheeler (1923) is restored by us. An insect species is subsocial if the parents care for their offspring during its development irrespective of whether direct feeding of larvae exists or not. Eusociality arises only in matrilineal communities, i.e. by the subsocial way. Parasocial way does not actually exist because (1) it contradicts to genetic interests of females that should become workers, (2) «parasocial (quasi- and semisocial) colony» is only temporary and facultative state of eusocial colony at the beginnings of its development or the result of casual errors in behaviour of solitary bees.

POLLEN FORAGING AND ALLOMETRIES AMONG STINGLESS BEES FORAGERS (APIDAE, MELIPONINAE)

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The small stingless bees foragers carry more pollen per unity of body weight than large ones. This relationship depends on allometric constraints with unknown adaptive effects both at community and specific levels. To test the hypothesis that this relationship remains true at colony level, foragers of *Melipona quadrifasciata anthidioides* were compared. The two colonies (weak and strong colonies) are characterized by the average body weight of their foragers (Table). Body weight is correlated with head and thorax width and tibia area also, than it's an estimator of body size and loading capacity of foragers. The amount of pollen grains per unit of a forager body weight (define as loading capacity = pollen load weight per bee body weight) becomes smaller as the body size increases (a strong negative correlation). The largest foragers exhibit the largest tibia also. Nevertheless, the tibia area and the pollen load weight are not correlated. So, other parameters, probably involving behavioral responses, seem to have a higher influence on loading capacity than corbiculae area. The production of smaller foragers by a weakened stingless bee colony should be an adaptive response because it increases the efficiency of pollen loading and gives rise to a faster recovery.

		bee weight (g)	Tibia area (mm ²)	Head width (mm)	Thorax width (mm)	Pollen load weight (g)	Loading capacity
Strong colony n=30	mean	0.08728	2.5403	3.9422	3.6419	0.00994	0.11386
	stdev	0.01311	0.1430	0.1174	0.0713	0.00551	0.08316
Weak colony n=30	mean	0.06399	2.1463	3.6839	3.4239	0.01099	0.17179
	stdev	0.00791	0.1135	0.0946	0.1183	0.00456	0.11862
Small foragers n=30	mean	0.08812	2.5089	3.9143	3.6113	0.00890	0.10104
	stdev	0.01247	0.1876	0.1554	0.1138	0.00547	0.07824
Large foragers n=30	mean	0.06315	2.1777	3.7117	3.4545	0.01203	0.19046
	stdev	0.00609	0.1474	0.1088	0.1341	0.00409	0.12830

CORRELATION $r_{0.05(58)}=0.254$					
	Tibia area	Head width	Thorax width	Pollen load weight	Loading capacity
Bee weight	0.738919	0.640999	0.584514	-0.552600	-0.71358
Tibia area		0.738407	0.645753	-0.20792	-0.41137

**NEST STRUCTURE OF LIOMETOPUM APICULATUM M.
(HYMENOPTERA , FORMICIDAE, DOLICHODERINAE)**

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Liometopum apiculatum is an edible ant in Mexico. People eat their immature cast named "escamoles", these are consider as a delicacy, used widely as food by many peasants or also sell in different restaurants at high prices, so there is a commercialisation. This habit comes from the prehispanic times and continuous today. Their nest was studied in different ecosystems that are: arid tropical scrub and pine-oak forest, It is composed by a set of galleries, chambers and trabeculas. Two of the societies studied had from 4 to 10 years of human exploitation and one of them were not exploited yet. Soils where they settled were of two types. The area cover oscillates from 6.30 m to 6300 m², and the volume goes from 5.63 m to 1890 m³ and the population from 218520 to 970789 individuals, being the biomass registered 10 K. to 44.5 K. The deepest found was 1.20 m. The chambers are not cimented, those that lodge the brood of the workers are little , measuring 0,5 to 2.75 cm., their number varies in these three nest from 28 to 79, having a temperature ranging in 22.5 ± 1 °C. The "Trabecula" (part of the nest where the "escamoles" are lodged) are 3 or more, they are localised near of the social surface (5 to 7 cm.) or down a stone . Their size varies from 17 to 70 cm. having a temperature mean of 24 ± 0.5 °C . This is different of the congeneric species L. occidentale var. luctuosum that have only one "Trabecula". The real chamber are farther of the " Trabeculas " this are localised down a big root of one tree or down a big stone, this chamber are highly humid and have the lesser temperature, 19°C is bigger than the other chambers for 1/3 to 2/3 more. The galleries varies in size and larger according, with the communication that make from 0.5 to 8.0 cm. of diameter, their temperature oscillates from 21 to 24°C. I All of this characteristics has permitted to this ant species survive after centuries of exploitation by man, forward as the people does not that it exists more than one / "trabecula" ,the peasants leaves the others and in this way the adults could mate and more foundations will be developed. L. apiculatum is monogynous and form polydomuos colonies.

First experiments on the diet of bumblebees (*Bombus terrestris* auct.)

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Methods generally used to determine nutritional requirements of *Apis mellifera* are based on the observation of parameters which cannot be used with *Bombus terrestris*. It was then necessary to develop an original method to allow nutritional test between several bumblebees diets. Thanks to this new method we investigate supplemented bumblebees diets. Bumblebees were offered regimes consisting of sugar syrup and pollen or sugar syrup supplemented with three apparently deficient amino acids (valine, isoleucine and methionine) and pollen. This supplementation don't increase significantly the productivity of the experimentals colonies and don't result in a significant increase in the amount of food consumed.

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L'EFFET DE LA TEMPERATURE SUR LES FORMICIDES EN DIFFERENTES AIRES AU BRESIL.

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Les formicides sont prédominants dans l'environnement, jouant un rôle diversifié, dès le contrôle biologique jusqu'au dommage économique. La recherche des facteurs influents dans la dynamique de ses populations peut fournir des subsides pour le contrôle ainsi que pour la préservation de ce groupe. Il y a des controverses de que la température n'affecte pas la dynamique des formicides dans les tropiques, où le climat est relativement constant. Les camponotines (*Camponotus*) ont démontré être dépendents de la température pour le développement de leur progéniture. Des appareils électroniques dont les températures varient de 25-30°C en moyenne, sont envahis par ce groupe. Ces appareils sont danifiés par une substance corrosive liberée principalement par les poupes et larves, dont les taxes de mortalité sont accentuées. En aire de cultive de *Citrus*, la température contribue avec 73,8% e 95,7% dans respectivement, la réduction qualitative et quantitative des formicides. Cependant en ecosystems agronomiques, la temperature de l'air n'a pas démontrée être un facteur limitant dans l'activité des populations des formicides. Néanmoins il y a des données, qui confirment que *Pheidole radoszkowslii* e *Solenopsis (Diplorhoptum)* sp. sont sensibles á temperature de l'air. Ainsi, des études especifiques dans des differentes temperatures controlées en laboratoire se font necessaire.

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LES NIDS DE *LABIOTERMES LABRALIS* (ISOPTERA: TERMITIDAE) EN FORET DE TERRE FERME EN AMAZONIE CENTRALE

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Les termites contribuent aux processus de formation du sol par la construction de leurs nids, qui sont rencontrés sur les arbres, dans le bois, ainsi que dans et au dessus du sol. En général, les nids constituent un système de chambres et galeries fermées, isolées des facteurs ambiants. Leurs aspects sont souvent caractéristiques et permettent de déterminer le genre et l'espèce. *Labiotermes labralis*, termite exclusivement humivore est une des espèces les plus abondantes en forêt primaire d'Amazonie Centrale (Apolinario 1993). Ses nids sont arboricoles, occupant les parties inférieures des troncs des arbres. Ils présentent une forme convexe et allongée, avec d'étroites galeries sur l'arbre qui sont le résultat d'une activité complexe de construction. Dans ce processus, un groupe d'ouvrier dépose les particules de sol, et un autre groupe intègre et dépose des excréments en un mouvement circulaire rapide de l'abdomen. Les chambres ont des formes allongées et aplaties, variant de 1.0-2.5 cm de hauteur sur 1.5-3.5 cm en largeur. La chambre royale se situe à proximité du centre du nid et mesure 2.5-4.0 cm de hauteur sur 3.5-5.0 cm de largeur. Sur une surface de 7.5-5.5 cm on peut trouver, en moyenne, 22 chambres. La superficie interne des chambres et galeries présente de petites rides sculptées, d'une manière qui est typique de cette espèce seulement (Emerson & Banks 1965). Parmi les 98 nids trouvés, avec des volumes variant de 2.507 à 163.091 cm³, il n'y a aucune relation significative entre la hauteur des nids et l'aire basale de l'arbre hôte. Ces informations représentent la première phase d'études expérimentales à long terme sur l'écologie et la dynamique des populations de cette espèce importante de forêt en Amazonie.

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POPULATION DENSITY OF *ANOPLOTERMES BANKSI* (ISOPTERA: TERMITIDAE) IN TERRA FIRME RAINFORESTS OF CENTRAL AMAZONIA.

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Humivorous *Apicotermitinae* ("soldierless termites") are typical of neotropical primary rain forest. The nests of *Anoplotermes banksi*, made from fecal matter, are found in the lower region of tree trunks, lianas, and palms, and also on fallen trees. *A. banksi* belongs to the most abundant species in Central Amazonian *terra firme* forests. The termites of 6 arboricolous nests of varying weight (92-2114 g) were separated into castes, counted and weighed (fresh weight). The colony size varied between 7576 and 39247 individuals, or 4.8 - 25.2 g of termites per nest. Average body weight was 0.89 mg, 0.26 mg, and 2.08 mg per worker, larva, and alate, respectively. Caste composition was generally about 1:1 for worker:larva; when alates were present (n=2) they generally accounted for 1.8-2.8% of the individual number. In small nests (n=5), we stated a positive correlation of the nest weight with total individual weight and weight and number of workers, respectively. However, nests weighing >2000 g (probably "senile" nests, Noirot 1969) show no such correlations, as their colony size tends to decrease due to natural mortality. Some large nests contained small amounts of individuals, however, no queen was found, and no external damage or predation was observed. With 18 nests per ha (Apolinário 1993), there are on average 38 individuals, or 24.3 mg of termites, per square meter. This species accounts for 18% of the termite nests of this rain forest, but for only 1% of the termite (animal) biomass.

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DEVELOPMENT OF SPATIAL ORIENTATION IN YOUNG *BLATTELLA GERMANICA* L. LARVAE.

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The aim of these experiments was to investigate the type of cues used in homing behaviour in young *Blattella germanica* L. larvae and how the use of these different types of cues intervene in the construction of spatial orientation. Several types of processes were tested : path integration with kinesthetic cues and visual orientation with landmark cues.

Tests measured the escape direction of larvae from the food box towards the shelter after a disturbance. Larvae were tested on one of the following days : day 1, 2, 3, 4, 5, 9, 10 or 11. Four experimental conditions were tested : A, kinesthetic cues and visual cues could be used by larvae; B, kinesthetic cues only could be used; C, visual cues only could be used and D, both types of cues were eliminated.

Either type of cue alone, (kinesthetic cue or visual landmark) was sufficient to allow larvae to orient towards their shelters, but they oriented more precisely when both types of cues could be used. When several landmark cues were present their relative angular position was important in the orientation process. From birth larvae were able to orient using path integration with kinesthetic cues. On the contrary they required 2 or 3 days to learn visual cues and to be able to orient correctly with this process. Spatial orientation was acquired gradually during the first days of the first instar through learning and maturation in relation to the presence or absence of different types of cues memorized through idiothetic or allothetic information. For the first time our results revealed day by day changes related to ontogenetic processes and different types of information the larvae could use to identify a particular place in their environment.

PERSISTENCE OF OLFACTORY CONDITIONED RESPONSES AFTER DIFFERENT CONDITIONING PROCEDURES IN THE HONEYBEE

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Olfactory learning performances in the honeybee have been extensively investigated using the conditioned proboscis extension response (CPE) on restrained individuals. The proboscis extension is a reflex (unconditioned response UR) spontaneously exhibited when the gustatory receptors of antennae, tarsi or mouthparts are contacted with a sugar solution (unconditioned stimulus US). This reflex can be conditioned by presenting an odor (conditioned stimulus CS) simultaneously to the elicitation of the UR and by enabling a food uptake (reward R). A conditioned response (CR) is then obtained with the CS alone. Different procedures of conditioning have been described, with one to several CS-US associations and different inter-trial durations. In order to investigate the persistence of the CR according to different procedures, we underwent conditioning with (i) one trial, (ii) three trials with 10 min inter-trials, (iii) three trials with 1 min inter-trials (mass trial). Caged bees were individually mounted at an age of 14 days, with their mouthparts and antennae free, and conditioned with linalool as the CS, 30% sucrose solution as the US and R. After the different conditioning procedures, the CR was tested at 9 times from 30 sec to 3 h, and then 24 h, 48 h, 72 h later. Independent groups of individuals were tested once for each period of time. It appeared that the proportion of individual exhibiting the CR was high and constant within 3 h after conditioning whatever the procedure applied (more than 70 % individuals responding). After 24 h, about 60 % of the individuals were still responding, the one-trial conditioning inducing the strongest decrease (down to 30 %). Responses were still obtained after 72 h, but at a low level for all 3 procedures (10-25 %).

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REPARTITION ET ABONDANCE DES TERMITES SELON UNE TOPOSEQUENCE EN FORET TROPICALE HUMIDE (TAI, COTE D'IVOIRE)

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Nos recherches se situent à l'intérieur d'un bassin versant en forêt primaire (parc National de Taï). La pluviométrie annuelle est d'environ 1800 mm. Notre échantillonnage est effectué selon la toposéquence, du sommet, au sol fortement gravillonnaire, vers le bas-fond sablo-argileux hydromorphe. Les nids épigés et arboricoles sont relevés à l'intérieur de parcelles de 1/4 ou 1/16 ha. Les nids souterrains sont échantillonnés par la fouille du sol de transects de 5 m de large selon la toposéquence et par des carrés de 1/2 m² dans les différents milieux. L'inventaire nous donne 44 espèces de termites, réparties en 30 genres. Ce peuplement apparaît équilibré, entre les Macrotermitinae (12 espèces), les Termitinae (19 espèces) et les Nasutitermitinae (7 espèces). Les humivores sont toutefois bien représentés dans ces biotopes (16 espèces). Les densités des nids épigés varient de 210/ha en mi-pente à 51/ha en bas-fond. Les espèces les plus abondantes sont *Thoracotermes macrothorax*, *Noditermes aburiensis*, *Cubitermes* sp. et *Cephalotermes rectangularis*. Parmi les Macrotermitinae, les nids de *Protermes minutus* dominent en mi-pente (110 nids/ha) et les nids de *Macrotermes ivoriensis* sont rencontrés uniquement sur les sommets (26 nids/ha). Les biomasses sont dominées par les espèces hypogées (58 à 76% des totaux, selon les milieux) et par les espèces de Termitinae, en majorité humivores (de 68 à 95% des biomasses, selon les milieux). Le milieu de sommet se distingue nettement par sa richesse en termites (biomasse totale de 19,12 g poids frais/m²). Les autres milieux montrent des abondances comparables aux données de la littérature (7,51 g/m² en mi-pente, 4,64 g/m² et 3,39 g/m² respectivement en bas de pente et en bas-fond). En effet, les résultats obtenus lors d'études similaires en forêt dense humide sont de 8,69 à 10,13 g/m² en Malaisie (Abé & Matsumoto, 1979), de 6,9 g/m² au Nigéria (Wood et al., 1982), de 11,0 g/m² au Zaïre (Maldague, 1964) et de 8,53 g/m² dans la forêt du Mayombe au Congo (Lepage et Rouland, non publ.).

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DNA FINGERPRINTING IN THE MONOGYNOUS AND POLYGYNOUS SIBLING SPECIES OF ANTS, *CAMPONOTUS NAWAI* AND *CAMPONOTUS YAMAOKAI*

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Using the ant-derived probe (pMy 7), we performed DNA fingerprinting in the monogynous and polygynous sibling ant species, *Camponotus nawai* and *C. yamaokai*. In monogynous *C. nawai*, band-sharing probabilities were low (mean: 0.09) between presumably unrelated individuals, but were consistently high (mean: 0.85) between workers of the same nest, suggesting that queens mated once and nestmate workers were super sisters. In polygynous *C. yamaokai*, band-sharing probabilities were low (mean: 0.13) between queens collected from different populations, moderate (mean: 0.25) between queens of different nests in the same population, but very high (within-nest means were 0.84 to 0.96) between queens of the same nest. Queens of polygynous nests seem to be genetically closely related (at least the level of sisters) with each other. Band-sharing probabilities between colony members sometimes reached to 1.00. It might results from intranidal mating (inbreeding) and adoption of the new queens into the natal nests.

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SPATIAL LEARNING AND EVOLUTION OF THE INDIVIDUAL FORAGING SPECIALIZATIONS IN A PONERINE ANT

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Three queenright colonies of the common neotropical ponerine ant *Ectatomma ruidum* Roger were connected with plastic tubes to a box containing live crickets as a source of protein, and to the center of an arena (diameter = 30 cm) from which foragers had access to three different honey sites placed 120° apart at the periphery of the arena. The location of the entry towards each honey site was indicated by a specific visual landmark (+, ● and ▲) placed above the entry of each corresponding tube on the inner wall of the arena. Foragers specialized into four behavioral categories which may be defined both on the basis of their fidelity to a given foraging site (crickets box, arena or honey sites) and according to their individual specialization in choice of food items. We distinguished: on one hand honey collecting workers and hunters consisting of two fundamentally different subsets of individuals according to their level of activity (specialists and hyper-active specialists), and on the other hand non-foragers and intermediates. In laboratory conditions, honey collecting workers show a high spatial fidelity and use visual cues to locate the site on which they specialize. The progressive familiarization of the foragers within the experimental device was studied by examining the directions taken by each individual after 5, 10, 20 and 40 days of observation. Workers foraging on honey show a more accurate visual orientation day after day toward the honey sites. For these honey collectors, and specially for the hyper-active specialists, both foraging efficiency (in terms of site fidelity and level of specialization) and activity level increase with learning over the 40-day period of training, while the performances of hunters are practically unchanged. Such learning abilities, combined with the control of time and place information by individual foragers (Schatz et al., 1994) appear closely related with *E. ruidum* foraging efficiency and account for their great flexibility in adaptive strategies (Passera et al., 1994) linked to a complex and fluctuating environment.

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HIGHLY EUSOCIAL TRAITS IN AN AUSTRALIAN ALLODAPINE BEE EXONEURA (EXONEURELLA) TRIDENTATA.

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Allodapine bees have frequently been regarded as exhibiting primitively social grades of organisation. This is partially due to their small colony sizes and the facultative nature of adult associations. However, one Australian species, *Exoneura* (*Exoneurella*) *tridentata* has a number of traits that are often associated with highly eusocial organisation. There is extreme body size variation among adult females accompanied by marked allometric differences between queen-like and worker-like females. Worker-like females show normal allodapine adult morphology, whereas queen-like females are much larger and exhibit a variety of distinctive morphological traits, including disproportional development of the genae and distal regions of the metasoma with dramatic enlargement of three apical 'teeth', and increased rugosity of the integument. Caste differentiation is evident at the 4th larval instar when future queens show markedly larger body size than members of their cohort. Virtually all females caught at flowers show normal morphology, whereas virtually all females observed guarding at the nest entrance show queen-like morphology. Queens frequently have such extreme wing wear that they are unable to fly; this wing wear probably arises from guarding activities. Queens are therefore dependent on worker-like females for provision of food. *E. tridentata* occurs in arid-zone mallee and mulga habitats and nests in beetle burrows in dead branches of several arid-zone tree species. Due to habitat aridity and physical characteristics of nesting substrates, branches used for nesting decay very slowly and may be used for many years by individual colonies. It seems likely that the extremely large body size of queens in *E. tridentata* is linked to the advantages that size confers on both guarding efficacy and reproduction. The evolution morphologically distinct, sedentary queens is probably facilitated by the utilisation of very durable nesting substrates, rather than the existence of large colony sizes.

THE RELATION BETWEEN GRAPE MEALYBUG AND ANT

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Grape mealybug is the most important pest of vine yards in kashmar city in Iran. The infested cluster of grapes are generally coated with a very sticky honey dew. The green raisins that is produced of such fruits is not dried well and will be undesirable.

Researches have shown that there is a clear relation between mealybug and ants so that the pest cannot act on the trees without the aid of ants. After hibernation stage, mealybug is brought from root region to the upper branches of vines and makes it to reach the clusters easily. In summer when mealybugs are active severely and secrete mass of honey dew on the wines, the ants use of it. In autumn when the hibernation stage start, mealybugs are taken down by ants to the roots and let them to get under the bark and inside the craks and holes. In a test that we killed many of the ants by using sevin on the wines, mealybugs could not continue to their activity and were controled.

HOST RECOGNITION IN *SPHECODES* PARASITIZING PRIMITIVELY EUSOCIAL HALICTIDAE

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S. monilicornis and *S. ephippius* females parasitize nests of the primitively eusocial halictid bee *Lasioglossum malachurum*. Visual, olfactory, and tactile cues are involved in stepwise nest recognition. First, visual cues of the nest entrance evoke hovering. In the following step, a landing reaction takes place, when visual cues are combined with olfactory cues, an adequate multicomponent odor bouquet. This behavior is followed by antennating the inner walls of the nest entrance tube. In this way, *Sphecodes* females are able to perceive substances of low volatility and the odor bouquet in its original composition, leading to the final nest entering reaction. A field bioassay was developed, offering artificial nests to passing *Sphecodes* females. Glass tubes were supplied with odorless or impregnated nest dummies, thus giving special attention to the olfactory cues that lead to host nest recognition. All tested extracts were also analysed by gas chromatography. Extracts of host nest entrances elicited entering reactions in the same intensity as did real nest entrances. The secretions of those glands that could be involved in composing the nest entrance bouquet were less attractive. However, the amount of the substances played a role. *Sphecodes* females distinguished between nest entrances of two different nest building halictids. The more similar the odor was to the host nest entrance bouquet in qualitative and quantitative composition, the more intense the reactions were. A mixture of synthetic alkanes and alkenes, imitating the composition found in nest entrance extracts, could also elucidate intense entering reactions. For host nest recognition, this mixture of hydrocarbons was sufficient.

DISPERSAL STRATEGIES IN A HEATHLAND
POPULATION OF *EXONEURA BICOLOR*.L.X. Silberbauer¹ and M.P. Schwarz²

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Nest founding in a heathland population of the Australian allodapine bee, *Exoneura bicolor*, occurs in two phases: an autumn dispersal phase and a spring dispersal phase. Females that fail to disperse in autumn spend winter in their natal nest; most spring dispersal occurs in late spring. The consequences of each of the two founding strategies was investigated using trap nesting techniques. The relative success of each of these founding strategies was examined by measuring: (1) the number of females within each sub-group that were alive at the end of the brood-rearing period, and (2) the number of brood in colonies from each sub-group and the pupal weight of the brood. Survival of females that founded nests in spring tended to be higher than that of females that founded nests during the preceding autumn, but autumn-foundresses had more advanced brood. There was a difference in the number of brood in colonies from each group; autumn-founded colonies had more brood than spring-founded colonies. Mean pupal weight from spring-founded colonies was significantly greater than in autumn-founded colonies. Wing length is a good indicator of body size. Mean population wing length decreases significantly between late summer and late winter, suggesting that smaller individuals suffer higher mortality during this period. It appears that spring-foundresses may produce fewer brood, but the larger body size of their brood could confer an advantage when they eclose as adults. This advantage becomes apparent in autumn and winter, when the smallest individuals suffer higher mortality than larger individuals.

ACID PHOSPHATASE ACTIVITY IN GLANDULAR CELLS OF DIFFERENT AGE BEES (HYMENOPTERA, APIDAE) ON SEVERAL SUBSTRATES.

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Using a modified Gomori lead salt method with sodium B-glycerophosphate, cytidine - 5'-monophosphate and trisodium trimetaphosphate as substrate, the acid phosphatase activity was investigated in the hypopharyngeal glands of *Melipona quadrifasciata anthidioides* Lep.. The distribution of the enzyme activity was dependent on the substrate. Contrary to the expected results the enzyme activity appeared only in the microvilli of the plasma membrane surrounding the intracellular canalicules, and is a prominent reaction in younger bees when using sodium B-glycerophosphate. The acid phosphatase in that region would be related to exocytosis process of secretion. With trisodium-trimetaphosphate as substrate, the reaction due to acid phosphatase activity was detected in the lysosomal organelle population and in the Golgi Complex with increased results in the glands of old bees. In this phase the cellular regression is a prominent aspect. Using cytidine -5'-monophosphate as substrate the acid phosphatase activity was demonstrated in both lysosomal and extralysosomal sites. These included myelin figures, resulting of degenerative glandular process, and secretory granules. In the glandular cells of old bees there was considerable amount of acid phosphatase in the canalicular lumen accompanying exocytosis of the secretion. No enzyme reaction occurred either on the glandular cells of newly emerged bees or in the case where the substrate was omitted from the incubating solution.

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ECO-FRIENDLY MANAGEMENT OF TERMITES IN BUILDINGS

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Subterranean termites are main source of termite infestation in buildings in India. Chlorinated hydrocarbons were found quite effective for soil tretment to control them. However, they are designated as highly toxic and environmentally stable. In order to find environmentally safe and ecologically compatible termite control measures for buildings, Chlorpyrifos is evaluated at various locations in India for soil treatment. Its concentrations from 0.25 to 2.0 per cent (a/i) are studied by (i) post-construction treatment in termite-infested buildings, (ii) modified ground board test and (iii) determination of residual toxicity of treated soil after different intervals. The study was started about five years ago and chlorpyrifos with 0.5 per cent concentration and above is still 100 per cent effective. However, in case of 0.25 per cent concentration, there was reappearance of termites in buildings after one year and also wooden baits in modified ground board test were slightly attacked. Availability of residue in the soil as determined by GLC was sufficiently high to keep it toxic. Similarly other environmentally friendly pesticides such as Endosulfan, Triazophos and Deltamethrin are also being studied. Further leaves, bark and flowers of some trees of Himalayan forests are extracted in polar and non-polar solvents. Extractives of leaves of some pine trees and bark of hard woods are found to have excellent termite - repellency.

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RAPDs AS A TOOL TO DISCERN POLYDOMY IN *FORMICA PALLIDEFULVA NITIDIVENTRIS*

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Nests of *Formica pallidefulva nitidiventris* occur in close proximity to one another along hiking trails in a Boulder city park. This study uses RAPDs (random amplified polymorphic DNA) to determine relatedness between nests, and thus polydomy. Thus far I have observed that workers in these clustered nests engage in internest movement and the foraging range for each nest often overlaps with those of neighboring nests. Internest movement has been observed as related to foraging in several other polydomous species (MacKay & MacKay, 1983; McIver, 1991). These observations suggest that these clusters of *F. pallidefulva nitidiventris* may be polydomous colonies whose workers tolerate one another's presence during foraging and in different nests and may be cooperating. RAPDs may be a better tool for discerning the number of nests occupied by a single colony, rather than relying on proximity or behavioral data, as polydomous nests can lack internest movement and be overdispersed (Traniello & Levings, 1986). As yet this study is preliminary, including only 10 nests belonging to 3 of the clusters observed, with one solitary nest used as an outgroup. The foraging observations were more thorough, conducted using 30 nests in 6 clusters plus 3 solitary nests.

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Sex pheromones and abdominal glands are preserved during evolutionary changes in cockroach mating behaviors

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Among cockroaches, there are three patterns of mating behaviors : **A** "female superior pose", **B** "male superior pose" and **C** "male and female in opposite positions" and two essential chemical signals : (1) sex pheromone released by one partner, generally the female (for long distance attraction), and (2) an aphrodisiac sex pheromone produced exclusively by male tergal glands (for female mounting and feeding behavior) (Sreng, 1993). In two closely related species of the Subfamily Oxyhaloinae, *Nauphoeta cinerea*. and *Gromphadorhina laevigata* (Roth 1971), contrary to what happens in other cockroach species, the males produce both of the main chemical signals : sex pheromone and aphrodisiac. The males possess complex sternal and tergal glands and in the mating systems, two different patterns of mating behavior (types **A** and **C**) occur. Comparative studies have been carried out on various mating patterns involving the abdominal glands but the sex pheromone components are known only in *N.cinerea* (Sreng, 1984; 1993).

The sex pheromone of the *N. cinerea*. (type **A** pattern) sternal gland is composed mainly of 3 compounds : 3-hydroxy-2-butanone, 2-methylthiazolidine and 4-ethyl-2-methoxyphenol (Sreng, 1990). These three compounds are also to be found in small amounts (about 1/40 of the sternal glands) in tergal glands licked by females. In *G. laevigata* (type **C** pattern), the results of GC and GC-MS analysis of abdominal glands have shown that the three compounds (3-hydroxy-2-butanone, 2-methylthiazolidine and 4-ethyl-2-methoxyphenol) present in the sex pheromone of *N.cinerea* are also present in tergal and sternal glands of *G. laevigata* but in equal proportions.

In type **A** mating, the tergal glands which are licked by females are well developed, whereas in type **C**, there is no licking of the male's tergal secretion by females, and the tergal glands are smaller (Sreng, 1984)

These 2 characteristics (Glands and sex pheromone components) provide a new clue for understanding species in which the morphology and mating pattern criteria are unrecognizable and establishing the evolutionary relationships between chemical signals, abdominal glands and different patterns of mating behavior.

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Two families of stingless bees, *Meliponae* from Pinar del Rio, Cuba and two families of *Trigonae* from Sao Paulo, Brazil were transported to Sweden for biological and practical studies. *Melipona bekeii Fulvipes* was found in western part of Cuba. After transferring into transport hives two colonies were sent by aircraft to Sweden via Madrid. After a flight of 15 hours in cabin, the bees were placed in an ordinary house with a temperature of +24 °C. Adaptation and beebiology was studied during a period of three years. A greenhouse experiment with tomato pollination was made during the summer of year two.

Adaptation of *Meliponae* was positive and after 10 days Scandinavian time was accepted. Development of colonies was good and the number of individuals increased from 800 to about 2000. Food was prepared from honey originated from Acacia. *Meliponae* refused acceptance of crystalised Swedish honey.

Biological studies was especially difficult, as the bees covered their nest with wax.

In order to achieve development- and behaviourstudies, medical gastroscopic instrument was borrowed from Academic hospital of Uppsala and was used with success. Observation of the colony was possible without disturbance of its behaviour.

The same technic was used for studies of two *Trigonae* colonies.

A more modern gastroscope equipment would probably have given a more sophisticated study of biology and behaviour.

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AGE-RELATED CHANGES IN POLYAMINE CONTENT IN *APIS MELLIFERA* NERVOUS TISSUE

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In vertebrates, the development of nervous tissue is partly controlled by polyamines, which plays role in nervous cell maturation, axogenesis, synaptogenesis and behavioural development. Since recent data pointed out that age-linked division of labour in adult worker honeybees is associated with substantial changes in certain brain regions (Withers et al; 1993), we analyzed polyamines in *Apis* nervous tissue. Polyamines, separated by reverse phase HPLC and detected by fluorescence were studied in 1-day-old, 7-day-old and 24-day-old adult foragers. Determinations were performed on optic lobes and brain minus optic lobes. In both brain parts, the putrescine levels were about 10 times higher than those of spermidine and spermine. However, whereas putrescine levels did not change in an age-dependent way, a large and significant decrease of spermidine and spermine titres occurred in both nervous structures, during the first week of adult life, reflecting drastic changes in polyamine metabolism throughout this period. Thereafter, only spermine levels significantly decreased, leading to an increase of the spermidine/spermine ratio, which could possibly be related to changes in the ratio of neuropile to cell body region. As compared to other data collected in an orthopteran (Strambi et al. 1993), our results indicated a specific pattern for polyamine distribution in *Apis* nervous tissue.

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A UNIVERSAL ELECTRONIC BEE COUNTER.

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An important parameter in evaluating the activity of a honeybee colony is given by the number of bees leaving and entering the hive as a function of time. The counter described here will permit to study more closely the effects of the environment (temperature, sun, rain, crop spraying by pesticides, etc...) on the behaviour and the survival of a bee colony. Beemovement is detected by means of 32 bi-directional channels. Movement detection inside a channel is effected via an infrared beam which hits a dual photoreceptor. The count results can be collected by a remote installed computer or read instantly on a LCD-display on the beecounter. A lot of registration have been done in the field under very different conditions: under normal weather conditions, on warm summer days as well on cold and stormy days, in presence of pesticides [1]. Reliability studies were set up by monitoring a bee hive in a closed fine-mesh wire cage. The counter appears to be well adapted to monitoring honeybee colony activity, even in the case of swarming since several successive swarms were registred. Flight cage tests gave a counting error less than 0.5%. The bee loss on cold and stormy days were sometimes dramatic (a loss of more than 20%). Immediately after spraying pesticides on a crop, the activity of the bee colony nearby became severely disturbed.

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POLYMORPHISM, POLYETHISM AND DIET BEHAVIOUR IN THE ANT, *MYRMICARIA OPACIVENTRIS* (EMERY) (FORMICIDÆ MYRMICINÆ)

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Myrmecaria opaciventris is a common species in the zone of the forest in Southern Cameroon. The morphologic study of this ant (light and scanning electron microscope) shows two main features :

i) Whereas the queen and the worker have a normal gaster, the shape of the gaster of the male is very different.

It is convex on the dorsal side and concave on the ventral side. The posterior margin of each sternite is V-shaped.

ii) The sting of the worker is spatula-shaped and striated. This spatula is used to spread the venom on the body of enemy. Then the venom goes through the integument to reach the nervous tissue.

The worker caste shows a monophasic unimodal polymorphism from the Wilson's classification. This variation in worker size (observed also in the first adults of a foundation) increases with colony population.

The study of polyethism in the worker responsible for tasks outside of the nest (defence and foraging of the colony) does not reveal a link to the morphology of the individuals. All sizes of workers are represented in every activity.

In the vicinity of the nest the foragers collect various alimentary pieces, among which Arthropods (mainly Insects) predominate. *M. opaciventris* completes its diet with honeydew originating from several species of Heteroptera, including Plataspidæ which are the most frequent.

THE EFFECT OF THE SIZE OF THE GROUP ON RESPONSES TO ANIMAL PREY IN WORKERS OF THE WOOD ANT *FORMICA POLYCTENA* FÖRST

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Responses to animal prey (dead houseflies) were studied in workers of the wood ant *Formica polyctena* kept in queenless and broodless groups ranging from 10 to 1000 individuals. In groups exceeding 35 individuals the workers, as a rule, kept to retrieve the flies to their nests until the end of the experiment (during 10 months). In contrast to that, in groups counting less than 35 individuals retrieval of the prey to the nest was observed only exceptionnally. In very small groups (less than 20 individuals) the responses of workers to flies were limited to antennal contacts, although general activity of the ants continued to be normal. The effect of group size on behaviour of workers of *F. polyctena* shown in response to animal prey was fairly flexible. When large groups were subdivided into smaller ones, below the "threshold size" of 35 individuals, the tendency to retrieve the flies to the nest gradually disappeared. The larger had been the initial group before its subdivision into smaller ones, the slower was the extinction of the tendency to retrieve the prey. When smaller groups were reunited into larger ones (over 35 individuals), the ants started to retrieve the houseflies already on the next day. Our present data demonstrate that workers of *F. polyctena* may continue to retrieve animal prey to their nests during many months even in the absence of a queen and of brood if they are living in sufficiently large groups. Our data show also that the effects of group size on responses of *F. polyctena* to insect prey may appear very rapidly, and that they are reversible. The effect of colony size on foraging and predatory behaviour in the ants is well known from many litterature data. Our present data demonstrate that group size has a profound influence on responses to prey also in queenless and broodless groups of ants.

THE XYLOPHAGOUS TERMITE (*NEOTERMES KOSHUNENSIS*) DEPENDING ON ATMOSPHERIC NITROGEN—AN APPLICATION OF STABLE ISOTOPE NATURAL ABUNDANCE METHOD

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In order to answer the question why xylophagous termites subsist on a diet containing only a little nitrogen, we studied nitrogen fixation of symbiotic bacteria in the gut of termites using the stable isotope techniques. We measured nitrogen stable isotope ratio ($\delta^{15}\text{N}$)[§] of a dry wood termite, *Neotermes koshunensis* Shiraki (Kalotermitidae, Isoptera), together with that of the food (nesting wood). $\delta^{15}\text{N}$ of the termites was lower than that of the food, showing different pattern as compared with other living things. We applied ^{15}N natural abundance method to the workers of termites, then the fraction of nitrogen derived from atmosphere ($\%N_{\text{dfa}}$) is given by the following equation ,

$$\%N_{\text{dfa}} = \frac{(\delta^{15}\text{N}_{\text{wood}} + \Delta_{\text{dig}}) - \delta^{15}\text{N}_{\text{sample}}}{(\delta^{15}\text{N}_{\text{wood}} + \Delta_{\text{dig}}) - \Delta_{\text{fix}}} \times 100 \quad (1)$$

where $\Delta_{\text{dig}} = \delta^{15}\text{N}_{\text{termite}} - \delta^{15}\text{N}_{\text{wood}}$ is the isotopic discrimination of nitrogen during the digestion of wood tissue and Δ_{fix} is that occurring as a result of nitrogen fixation. $\%N_{\text{dfa}}$ was calculated from the data of workers with the ranges of $\Delta_{\text{dig}} > 0$ and $-2 < \Delta_{\text{fix}} < 0$, which were assumed by the studies of stable isotopes. The results indicate that at least 30% and probably as much as 50% of nitrogen of workers of *N. koshunensis* comes from the atmosphere. Applying this method to various species of termites in Australia, it was observed that grass harvester termites which built a nesting mound scarcely utilized atmospheric nitrogen.

§ Natural abundance of ^{15}N is expressed in per mil deviation from a standard defined as the following equation (δ -notation) ;

$$\delta^{15}\text{N} = \left[\frac{(^{15}\text{N} / ^{14}\text{N})_{\text{sample}}}{(^{15}\text{N} / ^{14}\text{N})_{\text{standard}}} - 1 \right] \times 1000 \quad (\text{‰})$$

Atmospheric nitrogen ($^{15}\text{N} = 0.366\%$) is used as the standard.

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**REARING CERATINA CUCURBITINA (ROSSI)
(HYMENOPTERA, ANTHOPHORIDAE, XYLOCOPINAE)**

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The genus *Ceratina* Latreille was a long time considered as exclusively solitary (Michener, 1974) but presocial behaviours and existence of rudimentary castes are observed in several species (Michener, 1985; Sakagami & Maeta, 1987a, 1987b, 1989). In order to study social phenomenons, the authors have tried to rear *Ceratina cucurbitina*, the most frequent species of small carpenter bee in Europe. Nests collected in nature were placed into cages, in conditioned room. The authors have determined the optimal ecoclimatic, feeding and nidification conditions. The fly is observed between 20 and 36°C. However, between this extrema, the activity appears only in increasing temperature. The minimal illumination to observe activity is between 175 and 700 LUX. The light type seems indifferent (presence or absence of U.V. and I.R.). The copulation occurs mainly in decreasing atmospheric pressure.

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LIFE CYCLE AND SOCIAL ORGANISATION IN AN AUSTRALIAN ALLODAPINE BEE IN THE SUBGENUS BREVINEURA.

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The endemic Australian allodapine genus *Exoneura* contains three subgenera. At least several species in the subgenus *Exoneura sensu stricto* show unusually sophisticated forms of sociality involving well defined behavioural castes and kin association during cofounding of new nests. Another subgenus, *Exoneurella*, contains three largely solitary species and another species which appears to be highly eusocial. In this paper we describe the life history and social organisation of two species of *Brevineura*. Nest founding in *E. rufitarsis* appears to largely involve solitary females, but a high proportion of older nests contain two or more adults, with females exhibiting high levels of cooperative nesting and considerable size variation within colonies. The latter is associated with behavioural differentiation. Eggs are laid throughout most of the year and are attached to the nest wall until early larval stages. Most colonies contain a wide range of immature instars, and individuals can overwinter as eggs, larvae, pupae or adults. Reproductivity per female (the number of brood per adult female) increases significantly with the number of adults cooperating in nest use. Sex ratios are female biased and this may be due to local fitness enhancement (LFE), as suggested for *E.bicolor*¹, implying that factors leading to LFE may be widespread in Australian allodapines.

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DIFFERENTIATION OF BEHAVIOURAL CASTES IN THE PRIMITIVE
EUSOCIAL WASP *BELONOGASTER JUNCEA JUNCEA*
(HYMENOPTERA: VESPIDAE)

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Little is known about the biology of the *Belonogaster* spp. (Polistinae), this genus being peculiar to Africa, with, nevertheless, species recorded in Arabia and India.

With a view towards describing behavioural variability among individuals of *B. juncea*, we recorded the behaviour of 52 individuals belonging to four colonies at post-emergence. A multivariate analysis and, most notably, the analysis of principal components enabled us to discern four types of activity, including foraging, construction, feeding and reproduction. The reproductive caste is highly-individualized; the workers are differentiated into three sub-castes: foragers, builders and guards. The foragers are females who spend 82% of their time outside of the nest, supplying it with pieces of prey and liquid substances. The builders are foragers who tend to undertake construction activities. The guards are those females who spend most of their time on the nest.

The reproductive caste is limited to an individual with well-differentiated ovaries so that societies of *B. juncea* are monogynous.

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DIGESTIVE TRACT MORPHOLOGY OF *Acanthostichus serratulus* AND *Cylindromyrmex brasiliensis* (HYMENOPTERA: FORMICIDAE).

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Morphological studies of digestive tract of ants have revealed interesting and varied aspects among the genera as among the species of a genus, or among subfamilies. Two ants species of Cerapachyinae subfamily were studied as belonging to Ponerinae. However, the results showed that *A. serratulus* and *C. brasiliensis* have the morphology of digestive tract quite different when compared with species of Ponerinae subfamily. In these species, the morphological differences observed in digestive tract are related with the presence of a conspicuous furrow in the proventriculus, which is compounded by the mobile lips and elongated ventriculus. The digestive tract is both species is similar to two Mutillidae species particularly concerning to the ventriculus and the ileum. Thus, the special aspect of digestive tract seems to represent a primitive type among the ants. Our results agree with the opinion of BOLTON (1990), suggesting that Cerapachyinae species constitute a real subfamily and not tribes of Ponerinae.

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KIN AND GROUP SELECTION ANALYSES FOR DIMORPHISM IN THE PARTHENOGENETIC ANT *PRISTOMYRMEX PUNGENS*

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In the myrmicine ant *Pristomyrmex pungens*, there are no winged queen castes and workers (morphologically defined) reproduce parthenogenetically. Most colonies have monomorphic workers. However, distinctly large workers have been found sporadically in some colonies that have four ovarioles, rather than two found in "normal" workers. Large workers exceed normal workers in the reproductive capacity and probably have higher fitness than normal workers on a within-colony level. However, large workers reduced a colony's fitness at the between-colony level. So there was conflicting phenotypic selection between colony and individual levels, and large workers may be socially parasitic phenotypes. I used two quantitative genetic models, Price's partitioning of covariance (a group selection model) and Queller's general kin selection model, to predict the evolutionary consequence shaping the frequency of worker types. All workers can be reproductive and live only one year. Thus, annual colony growth ratio measured the mean individual lifetime reproductive success. With-colony individual variation in reproductive activity was estimated from individual ovarian development. Preliminary estimations of heritability were also obtained. Both analyses indicated similar conclusions that large workers will not be widespread in the entire population, unless the heritability at within-colony level is high or within-colony relatedness is very low.

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A MATHEMATICAL APPROACH OF LIFE HISTORICAL COMPARISON BETWEEN MONOGYNY AND POLYGyny IN ANTS

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There are two main modes of colony founding in ants; 1. Queens start new colonies without the aid of workers (independent founding, monogyny). 2. One or several queens leave their natal nest accompanied by workers and establish a new colony (dependent founding, polygyny). Independent founding queens suffer a high mortality and take longer time for the colony to grow up until producing the first sexual brood, while dependent founding queens can reach their maximal fecundity earlier. Queens of monogynous species generally have a longer life span than those of related polygynous species(1). Keller has compared monogyny and polygyny through life time reproductive success(2). This means that he has implicitly assumed a stable population. It is difficult to assume that all ants live in stable environments. Theories of life history strategy suggest that if population is increasing, the fitness is more appropriately measured by the intrinsic rate of natural increase (r). In an increasing population, it is important determinant of fitness when individuals begin their initial reproduction. The theory has been originally applied to non-social organisms. Here we introduce it to polygyny in ants, and indicate that a dependent strategy evolves more easily in an increasing population than in a stable population. We do not refer to conflicts among individual colony members, because our model assumes asexual reproduction. We make explicit discussions of how the population demographic parameters are important for the evolution of social behaviour.

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ATTRACTANTS, REPELLENTS, AND PHEROMONES: INNOVATIVE CONTROL OF PEST ANT POPULATIONS

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The fire ant, *Solenopsis invicta*, is a medical and agricultural pest in the Southern United States. Over the last several decades control methods have been developed for the fire ant that have had applicability to other pest ant species, thus the fire ant is a good model system. My research has centered on the investigation of fire ant behavior and the chemistry associated with that behavior. The objectives are to use this knowledge to develop control methods that decrease the amount of insecticide placed in the environment and to make control methods more species-specific. Two methods of achieving these goals are considered here. One is to use a worker attractant pheromone to decrease the time it takes for a worker to discover bait particles and to increase the probability of making the discovery. The other method is to exclude the fire ant from areas where it is not wanted through the use of repellents. Exclusion has direct applicability for the protection of electrical equipment to which the fire ant is attracted. Several classes of repellent have been discovered using a Y-tube olfactometer (carboxylic acids, alcohols, esters, alkenes, and alkynes). These compounds are characterized by being very volatile; therefore, to prolong their effectiveness they must be formulated for controlled release. We have achieved this goal by utilizing Hercon Environmental, Inc. "Sandwich" technology to slow the repellent release rate to obtain effective repellency for over nine months. This longevity of activity is a prerequisite to ultimate commercialization. There are several fire ant pheromones that elicit worker attraction, e.g. recruitment and queen recognition pheromones). Using a component of the queen recognition pheromone we have demonstrated that workers find bait particles quicker if the bait is enhanced with an attractant pheromone. In addition, evidence indicates that the ant also finds a higher percentage of the bait particles. Hypothetically this will decrease the probability of non-target ant species getting bait particles, thus making the bait more species-specific.

EVALUATION OF NEWER TERMITICIDES FOR EUCALYPT PLANTATION ESTABLISHMENT

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Among the forest plantation crops, eucalypt is most vulnerable to attack by termites in India. If protection is not given, large-scale mortality of seedlings takes place during the initial establishment phase. Until recently the standard practice was to drench the basketted seedlings, prior to planting out, with aldrin, heptachlor or chlordane but these organochlorine insecticides have now been banned. Alternative, less persistent insecticides were therefore tested. These included chlorpyrifos, the synthetic pyrethroids-cypermethrin and fenvalerate and neem seed cake.

The experiment was laid out in a randomised complete block design with 3 replicates of 50 seedlings each. Before planting out the basketted seedlings were treated with the required quantity of the insecticide by group-drenching. Neem seed cake was mixed with the potting soil. The data collected for the first six months are presented.

Preliminary results indicate effectiveness of chlorpyrifos, cypermethrin and fenvalerate. Neem seed cake (both oily and deoiled) did not prevent termite attack. The observations are continuing.

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REGULATION OF THE CHEMICAL SIGNATURES OF TWO TERMITE SPECIES, *RETICULITERMES SANTONENSIS* AND *RETICULITERMES GRASSEI*, LIVING IN A MIXED EXPERIMENTAL COLONY.

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Each of the 2 species *Reticulitermes santonensis* and *R.grassei* has its own distinctive chemical signature, which subserves intra-species recognition (Bagnères et al., 1990, 1991b). When the 2 species were experimentally kept in mixed colonies, their chemical signatures underwent a change, as is known to occur in the case of mixed ant colonies (Bagnères et al., 1991a). The first detectable signs of the change occurred as early as 2 hours after the 2 species were first brought together. Each species acquired the cuticular substances which are specific to the other species, but the quantities acquired by *R.grassei* were larger than those acquired by *R.santonensis*. The 2 signatures were not simply juxtaposed. The results of a multivariate analysis showed that although *R.grassei* acquired the hydrocarbons specific to *R.santonensis* in the same proportions as those present in the *R.santonensis* control individuals, *R.santonensis* did not acquire the *R.grassei* hydrocarbons in the same proportions as those present in the *R.grassei* controls. Nor did the proportions of original hydrocarbons specific to either *R.santonensis* or *R.grassei* individuals remain the same after exposure to the other species.

The results obtained with this model for an experimentally mixed heterospecific colony suggest some hypotheses about the regulation and production of hydrocarbons, and about the exchanges occurring between individuals living in the same colony.

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COMPARATIVE STUDIES ON *APIS MELLIFERA* AND *APIS CERANA* UNDER SOUTH INDIAN CONDITIONS

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Brood development followed similar pattern in both the species, reaching maximum during October – November and minimum in June-July. *A. cerana* activity started early around 7 AM and went upto late in the evening, whereas *A. mellifera* activity started around 9 AM and stopped before 5 PM. Peak activity for both was between 9-11 AM. *A. cerana* sustained with low available forage and had wider host range. *A. mellifera* population declined drastically during lean period unless supplemented with food and did not visit all the flora visited by *A. cerana*. In addition *A. mellifera* suffered with brood mite, *Tropilaelaps clarae* and periodical treatment with sulphur was necessary. *A. cerana* did not have this problem but suffered heavily from Thai Sac brood disease. *Varroa* was not a problem for both the species. Wax moth did not invade *A. mellifera* boxes, but was an occasional problem in *A. cerana*. *A. mellifera* did not fare as well as *A. cerana* in honey collection from *Eucalyptus*, *Pongamia* and rubber plant (*Haevia* sp.) but did better on sunflower. Bee eater (*Merops* sp.) was a big menace to *A. mellifera* in some parts of Southern India, particularly Kottayam district of Kerala, but not on *A. cerana*. All the four species of honey bees including *A. dorsata*, *A. cerana*, *A. florea* and *A. mellifera* foraged together with no inhibition. There was no indication of any bad effect from any of the four species when occurred in the same locality. From four years study, it can be said that *A. mellifera* has certain limitation to establish itself without the aid of human being under South Indian conditions.

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SIMILARITIES AND DIFFERENCES BETWEEN ENDO- β -1,4-GLUCANASE ACTIVITIES FROM *MACROTREMES* SPECIESP.C. Veivers¹, M. Slaytor¹ and R. H. Leuthold²¹Department of Biochemistry, The University of Sydney, Sydney, N.S.W. 2006, Australia. ²Abteilung für Neurobiologie, Universität Bern, CH-3012, Switzerland

Endo- β -1,4-glucanase activity was measured in the guts of four categories of worker caste termites (young and old, major and minor) of *Macrotermes bellicosus*. No significant differences were found between young and old categories (minor workers 7.36-9.65 mg glucose/termite; major workers 14.74-19.37 mg glucose/termite), similar to results for *M. michaelseni* but different from *M. subhyalinus* where the activity in young worker castes was significantly greater than the activity in old categories of workers (Veivers et al., 1991). Endo- β -1,4-glucanase activity in the fungal nodules associated with *M. bellicosus* (4.87 ± 0.47 μ g glucose/mg wet wt) was similar to that in *M. subhyalinus* (4.34 ± 0.24 μ g glucose/mg wet wt) but lower than in nodules from *M. michaelseni* (8.22 ± 0.86 μ g glucose/mg wet wt)¹. Endo- β -1,4-glucanases separated from fungal nodules of *M. bellicosus* and *M. subhyalinus* were multicomponent with similar elution profiles on Bio-Gel P150 chromatography. Under these chromatographic conditions endo- β -1,4-glucanase activity from *M. michaelseni* fungal nodules consisted of one component. Chromatofocussing of fungal nodule extracts from *M. bellicosus* on PBETM 94 revealed a pattern of endo- β -1,4-glucanase activities with similar pI values to those found in *M. natalensis*². Comparison of elution profiles on Bio-Gel P150 of termite and fungal endo- β -1,4-glucanase activities from *M. bellicosus* and *M. michaelseni* indicates that endo- β -1,4-glucanase activities present in termite gut extracts are different from those in the associated fungal material, i.e. fungal nodule endo- β -1,4-glucanase activities are not acquired by the termites.

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SIMILARITIES AND DIFFERENCES BETWEEN NORTHERN EUROPEAN AND MEDITERRANEAN URBAN ANT FAUNAS — A MULTILEVEL HYPOTHESIS

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A previous study (Vepsäläinen and Pisarski 1982) on urban ant faunas showed higher turnover rates of species than did surrounding rural ant faunas along a north-south gradient from northern Finland to central Poland. The urban faunas of the two extreme ends of the gradient, Kuusamo and Warsaw, did not share a single species, although all Finnish species known along the gradient occur also in Poland. However, on a higher level of analysis, similarities among the urban ant faunas emerged: Urban ant species tend to be ecological ubiquists that are common and abundant in the dominating habitats around the town; they also tend to be ecological generalists but poor competitors, and pioneer species of early successional environments. Secondly, species that are regionally met exclusively in towns are of more southern origin, which is understandable as towns are warmer and drier than the neighbouring natural environments. In the present poster we extend our generalization from northern Finland (Lapland) to the Mediterranean region. I suggest that also in the Mediterranean areas, urban ant faunas are overrepresented by species characterized by the same ecological attributes as summarized above. However, if any exotic urban species are met in Mediterranean towns, I expect them to represent species of more northern origin. The expectation springs from microclimatic differences between towns and the Mediterranean rural areas: they tend to be opposite to the differences in more northern areas, so that — given any differences do exist — towns are cooler and moister. The scarce literature available supports the hypothesis (Bernard 1958, 1974; Passera 1977), but specific data tailored to test the hypothesis are still needed.

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CONGRUENCY OF HYDROCARBONS PATTERNS IN HETEROSPECIFIC GROUPS OF ANTS: TRANSFER AND/OR BIOSYNTHESIS

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In homospecific groups of ants, each species has its own profile of cuticular hydrocarbons which are commonly considered as nestmate recognition cues. When reared together in bispecific groups, workers of both species acquire the hydrocarbons of each other. The aim of the present study was to investigate the way(s) of formation of this mixed odor in artificial groups *Formica selysi*/*Manica rubida* and *Formica selysi*/*Myrmica rubra*. The *de novo* biosynthesis of hydrocarbons and their transfer between workers was demonstrated by an *in vivo* radiochemical assay using [¹⁴C] sodium acetate. Labeled hydrocarbons were found on the cuticle and in the postpharyngeal gland of the injected ants. The transfer of labeled hydrocarbons between nestmates (homospecifics in control groups and heterospecifics in mixed groups) occurs passively by body contacts and actively by trophallaxis and grooming. The ability of one species to synthesize *de novo* the hydrocarbons of the other species was also investigated. The relative contribution of the transfer and the *de novo* biosynthesis in the constitution of the mixed odor is discussed.

SILK NESTS OF CAMPONOTUS SPECIES IN THE TROPICAL RAIN FOREST OF SOUTH EAST ASIA

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Weaver ants use larval silk to construct nests. This fascinating behaviour independently evolved in four genera (*Dendromyrmex*, *Polyrhachis*, *Oecophylla* and *Camponotus*). The result is a great number of different constructing strategies and nest types. Recently some new species of the *Camponotus* subgenus *Karavaievia* could be found in Malaysia, three of them (*C. texens*, *C. orinus* and *C. gombaki*) were compared with regard to their construction principles and the pavilion types they prefer. Additional biological and ecological data were recorded. We found more than 20 different kinds of pavilions, obviously influenced by the given leaf structures of the nesting trees. *C. texens* builds simply constructed silk pavilions weaving leaves together without any alterations to their form or size, whereas *C. gombaki* changes the given leaf material to a slight extend. The most complex form of woven pavilions could be analysed in *C. orinus* colonies. They form pavilions with pure silk layers that give extremely dry shelter to the cocoons stored inside.

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ORIGIN OF MALES IN ANT POPULATIONS

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The reproductive division of labor is one of the most prominent features of social insect colonies. In many species, however, workers have retained their capability to produce male offspring. Worker reproduction is expected to vary as a function of colony structure and worker produced males should be found in monogynous, monandrous colonies only. In this study the relatedness between workers and males in different ant species were estimated using allozyme analysis to test whether the queen(s) or workers were responsible for male production. Preliminary results of our group suggest that males are produced by queens at least in some populations of *Formica truncorum*, *Myrmica ruginodis* and *M. rubra*, but the possibility of worker reproduction cannot be completely ruled out. More data will be collected and analyzed during the summer 1994.

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SEASONAL PATTERNS IN *RETICULITERMES*
(ISOPTERA; RHINOTERMITIDAE) IN A TIDAL
WETLAND HABITAT IN VIRGINIA

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Reticulitermes spp. colonies remain above-ground year round along the coast on the Eastern Shore of Virginia. Field measurements and laboratory experiments to determine seasonal rates of nitrogen fixation (acetylene-reduction) related to temperature and food quality were performed over a year on termites collected from logs. In the field, nitrogen-fixation (acetylene-reduction) rates measured for termite workers were highest during moderate temperatures in the autumn and lowest during hot summer and cold winter months. In laboratory experiments, nitrogen-fixation rates were significantly higher when termites were incubated at 26°C than at 22°C or 32°C. These results indicate that the nitrogen contributions of *Reticulitermes* to forest habitats are temperature-dependent and vary seasonally. Termites endured log temperatures as low as 2.1°C, and termite-infested logs were occasionally submerged in brackish water during high tides.

TROPHIC NICHE OF TWO STINGLESS BEE SPECIES OF THE GENUS *MELIPONA* AND THE AFRICANIZED HONEYBEE (*APIS MELLIFERA*) IN ATLANTIC FOREST OF SÃO PAULO STATE, BRAZIL

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The trophic niches of the native Atlantic Forest species *Melipona quadrifasciata anthidioides* and *Melipona bicolor* and the introduced *Apis mellifera* were studied by pollen analysis at the Estação Biológica de Boracéia, located in nearly undisturbed rainforest with a few patches of secondary growth. The *Melipona* species were chosen for a comparative study with the introduced *A. mellifera* because they represent stingless bees of approximately the same size, are thought to be polylectic like the honeybee and in a bee survey they were found to be common at that site. During the same survey, *Apis mellifera* was shown to be one of the most abundant species. The study was conducted with two colonies of each species and incoming pollen was collected two to three times per month over a period of one year. Honey was analyzed once per month and also stored pollen of the *Melipona* species. The results show that for pollen *M. quadrifasciata* and *M. bicolor* relied heavily on Myrtaceae and Melastomataceae but made little or no use of other types of pollen heavily collected by *Apis mellifera*, such as *Didymopanax* (Araliaceae), *Vernonia* (Asteraceae), *Ilex* (Aquifoliaceae), *Croton* (Euphorbiaceae) and palms (Arecaceae). For nectar the spectrum of visited plants by the *Melipona* species is larger and also includes Asteraceae, Rubiaceae, Fabaceae and Cunoniaceae. The overall result is that there is only a partial overlap between the diets of the *Melipona* species and *Apis mellifera*. Despite the fact that the *Melipona* species are polylectic and are able to collect various types of pollen, they apparently make little use of this ability. They thus show a very different pattern in comparison with *Apis mellifera*, which rapidly switched from one main pollen source to another.

RESPONSES TO NEST DAMAGE IN THE AFRICAN WEAVER
ANT *OECOPHYLLA LONGINODA* (LATREILLE)

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Responses of the African weaver ants *Oecophylla longinoda* to nest damages were studied in the field in Nigeria. During the wet season, the ants responded to nest damages almost unexceptionnally by a quick onset of nest-repairing behaviour. The latencies to the start of nest-repairing activities (LN) did not depend on the size of the damage, but they were significantly shorter during the night, and positively correlated with ambient temperature. During the dry season, the ants responded to large nest damages mainly by abandoning the nest. In the case of medium size damages, the onset of nest -repairing behaviour was equally rapid as during the wet season, but in the case of small damages it was sometimes greatly delayed (up to three hours). The values of LN did not differ between the nighttime and the remaining times of the day, and they were not correlated with ambient temperature.

CAPTURE AND RETRIEVAL OF VERY LARGE PREY BY WORKERS OF THE AFRICAN WEAVER ANT, *DECOPHYLLA LONGINODA* LATREILLE

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We report numerous (n = 202) cases of capture and/or retrieval of very large prey by workers of the African weaver ant, *Decophylla longinoda*, observed in Cameroon, Nigeria and Zaire. In particular, we report 18 cases of group transport of vertebrates (frogs, lizards, snakes, birds and rodents). We describe also the remains of 16 vertebrate prey items (lizards, snakes, birds and bats) found in the nests of *D. longinoda* in South Cameroon. Previously, retrieval of vertebrate prey was reported only once in the Asian weaver ant species, *D. smaragdina* (Hingston, 1927). Retrieval of large prey was exclusively observed in workers of large, mature colonies of *D. longinoda*, occupying solitary trees or bushes or groups of trees. As demonstrated by field and laboratory tests, *D. longinoda* capture large insects most efficiently while hunting in the manner of army ants. Our observations showed also that large arolia on the feet of workers of *D. longinoda* are of crucial importance for the success of capture and transport of large prey. Thanks to these structures, a single worker of *D. longinoda* can immobilize a struggling insect much more larger than itself, such as, for instance, a praying mantis, or held suspended a dead bird weighing 7 grammes.

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INVESTIGATION ON ANT FAUNA (HYMENOPTERA: FORMICIDAE) OF WUHAN CITY (I)

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14 species of ants are described with their pictures and photos. They are Brachyponera chinensis(Emery), Iridomyrmex glaber Mayr, Pheidole nodus Smith, Pristomyrmex pungens Mayr, Messor aciculatus(Smith), Crematogaster contentior Wheeler, Tetramorium caespitum (L.), Tetramorium kraepelini Forel, Monomorium chinense Santschi, Paratrechina sharpi (Forel), Paratrechina bourbonica (Forel), Camponotus japonicus Mayr, Camponotus quadrinotatus Forel, and Formica japonica Motschulsky. Five of them, Brachyponera chinensis, Iridomyrmex glaber, Pheidole nodus, Tetramorium caespitum, and Paratrechina bourbonica, invade and inhabit houses and public buildings, while Paratrechina bourbonica can nest on as high as the 7th floor. Nine species, Iridomyrmex glaber, Pheidole nodus, Pristomyrmex pungens, Crematogaster contentior, Tetramorium caespitum, Paratrechina sharpi, Paratrechina bourbonica, Monomorium chinense, and Camponotus japonicus, have commensal relations with aphids and coccids. The nesting activity of Pheidole nodus, Messor aciculatus, Tetramorium caespitum, Camponotus japonicus, and Formica japonica may damage the structure of a grassland. Crematogaster contentior normally nests in holes and cracks of a tree trunk.

DIFFERENT EVOLUTIONARY CONDITIONS FOR WORKER AND SOLDIER CASTES EXPLAIN CASTE DISTRIBUTION AMONG ALL EUSOCIAL INSECTS

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In eusocial wasps and bees, each species has only one sterile caste, termed worker, where workers engage mainly in caring and foraging for eggs and larvae, although they occasionally defend their colonies against predators. In most ant species, there are only worker castes similar to those in wasps and bees, while some species have additional castes, termed soldier. The soldiers defend their colony and colony members against attacking enemies, but neither collect the food nor care for the young. In termites, almost all species have more specialized soldier castes, where soldiers must be fed by other colony members. Some groups, called higher termites, have sterile worker castes as well, while other groups, called lower termites, lack such true worker castes although nymphs before maturation take the role of workers. Yamamura (1993) suggested that the evolution of worker and soldier castes must be considered in terms of different trade-offs, specifically, the different relations between benefits and costs of sterility. An individual should be a sterile worker if the genetic gain of raising its sibling is higher than the genetic cost of losing its own offspring, while an individual should be a sterile soldier if the sacrifice of its own life is genetically compensated for by the survival of other family members. Thus, asymmetry of relatedness to offspring and sibs is most important in worker evolution, assuming the origin is a subsocial family, while the average relatedness to colony members in soldier evolution. Applying these different conditions for evolution of sterility, caste distribution among existing eusocial insects can be explained by a difference in genetic systems: Aphids and a parasitic wasp with asexual reproduction have only the soldier caste; wasps, bees, and ants with male haploidy have mainly the worker caste; and termites with diploidy have dominantly the soldier caste. New findings of eusocial gall thrips with the soldier caste and an ambrosia beetle with the worker caste also support the above theoretical model.

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ETUDE COMPARATIVE DES RÉGIMES ALIMENTAIRES DE QUELQUES ESPECES HUMIVORES DE SAVANE

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Il est généralement admis que les termites humivores se nourrissent aux dépens de la matière organique mélangée au matériel minéral du sol. Le rôle de ces espèces se traduit par le remaniement d'importantes quantités de sol et surtout par les modifications physico-chimiques du matériau en place. L'impact des termites sur la matière organique du sol et sa distribution dépend de la répartition des espèces dans le profil de sol et des transformations opérées sur les substrats consommés. Notre étude constitue l'une des premières tentatives pour mettre en évidence des régimes alimentaires différents chez plusieurs termites humivores de savane humide, selon la nature des substrats dégradés dans le tube digestif. D'autre part, nous mettons en relation ces régimes avec la qualité de la matière organique liée à la répartition des espèces dans le profil de sol. Pour atteindre ce double objectif, nous utilisons à la fois les techniques d'échantillonnage de la mésofaune endogée et les méthodes d'étude du métabolisme digestif. Quatre espèces sont étudiées, dont deux à nid épigé (*Cubitermes subcrenulatus*, *Promicrotermes holmgreni*) et deux à nid hypogé (*Basidentitermes potens*, *Astratotermes* sp.). Les détections enzymatiques montrent pour toutes les espèces, sauf pour *Astratotermes*, de fortes activités osidasiques. Les polysaccharides les mieux dégradés sont l'amidon, la laminarine et la lichénine. *Cubitermes subcrenulatus*, *Promicrotermes holmgreni* et *Basidentitermes potens* ont des activités cellulaisiques relativement importantes (par rapport aux espèces humivores de forêt), mais faibles par rapport à celles précédemment trouvées par d'autres auteurs chez les termites xylophages. Le classement des substrats testés en fonction de leur origine végétale, couplé avec les résultats des activités enzymatiques selon les catégories de substrats ainsi définies, a permis de ranger les espèces étudiées selon trois régimes alimentaires différents. Ce sont tout d'abord les consommateurs de matière organique d'origine diversifié (matériel végétal épigé ou racinaire), représentés par les espèces épigées (*Cubitermes*, *Promicrotermes*). Ensuite, nous distinguons les consommateurs de matière organique préférentiellement d'origine racinaire (matière organique fraîche), représentés par l'espèce *Basidentitermes potens*, qui occupe la strate superficielle du sol au niveau des racines et radicelles des touffes de Graminées. Enfin, les consommateurs de matière organique ancienne ou polymérisée, représentés par l'espèce *Astratotermes*, dont la répartition se situe dans les couches profondes du sol. Ce travail préliminaire doit être complété par une caractérisation biochimique de la matière organique consommée et par une étude écologique de la répartition des espèces au cours de la saison.

Référence

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ANTS AS NATURAL ENEMIES OF THE ARARAT COCHINEAL

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Ararat cochineal (*Porphyrophora hamelii* Brandt) is a rare endemic species of the Ararat plain included in the Red Data Book of the former USSR. At present the existence of this insect is under a threat that is explained mainly by the cultivation of saline lands, i.e. habitats of cochineal. According to the observations of Mkrtchian and Sarkisov (1985) different developmental stages of *P. hamelii* are used as a food source by some vertebrates and invertebrates (they have indicated four species of ants - *Tapinoma erraticum*, *Messor caducus*, *M. structor* and *Pheidole pallidula*). However, the species list of cochineal ant enemies remained incompletely known and the impact caused by the ants on this species was not evaluated. Present research was carried out during 1988-1992 in the territory of the Ararat cochineal reserve (Echmiatsin region in Armenia). To take a census of ant nests the method of Dlussky (1965) has been used. The numbers of cochineals that were brought to nests have also been counted (observation periodicity - 1 h, duration - 15 m). The observations indicated that various species of ants during the whole period of *P. hamelii* going-out (from the beginning of September to the end of the 1st decade of October) captured the imago of cochineal at 1 ha in the following numbers (first is the number of females /second of males): *Messor caducus* (42900/2325), *M. structor* (62020/3255), *Pheidole pallidula* (5250/780), *Cardiocondyla Bogdanovi* (28560/4920), *Monomorium ruzskyi* (45870/6930), *Tetramorium caespitum* (19440/3120), *Tapinoma erraticum* (33235/4420), *Cataglyphis aenescens* (88605/7695), *C. nodus* (14301/833), *Formica cinerea armenica* (4983/402). Total numbers of cochineals captured in all ant nests per ha were 345164 females and 34680 males, their weight being in sum correspondingly 9086 and 69 g. It is worth to note that some species of ants (*Tetramorium caespitum*, *Monomorium ruzskyi*, *Cardiocondyla bogdanovi*, *Leptothorax satunini*, *Tapinoma erraticum*, *Plagiolepis pallens*) captured cochineal larvae as well. The estimation of ants impact on the population of *P. hamelii* is of certain interest in connection with the elaboration of conservation measures for this rare insect.

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POLLEN SPECTRUM OF SOME HONEYS OF JAMMU AND KASHMIR, INDIA, AS DETERMINANT OF HONEYBEE FORAGE

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Melissopalynological studies were conducted on 25 honey samples collected from Indian hive bee, Apis cerana F. colonies located in different parts of Jammu and Kashmir with varying altitudes and climatic conditions. These investigations revealed that dominant sporomorphs were of Salix sp., Fagopyrum sp., Plectranthus sp., Trifolium sp., Portulaca sp., Brassica sp., Albizia sp., Acacia sp., Taraxacum sp., Robinia sp., Aesculus sp., Bidens sp., Rumex sp. and Impatiens sp. The minor pollen components represented in these honey samples were of Berberis sp., Potentilla sp., Artemisia sp., Helianthus sp., Salvia sp., Ageratum sp., Acer sp., Bauhinia sp., Polygonum sp., Origanum sp., Pyrus sp., Prunus sp. and members of families Lamiaceae, Brassicaceae, Asteraceae, Sapindaceae, Poaceae, Rosaceae and Myrtaceae. Present studies revealed both uniflorality and multiflorality in different honey samples. On the basis of these studies, a floral calender of 175 honey plants of Jammu and Kashmir, indicated their taxonomic status, geographic location, honey potentiality, periods of flowering and economic uses has been prepared. Present studies can be helpful for setting up new apiaries in migratory bee keeping practices and application of modern bee management technology.

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THE TREE AND THE ANTS

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This is a film, 52 minutes long, whose principal theme is the relationship between ants and plants and which also presents some scientific results not previously made public. One can see, for example, the Ponerine ant *Platythyrea Corradti* which uses superficial forces to harvest and transport nectar. The co-evolution of caterpillars and ants is demonstrated by showing, on the one hand, several defensive strategies employed by caterpillars and, on the other, the mutualism between caterpillars and ants as regards *Lycaenidae* and *Noctuidae*. The most surprising case involves caterpillars of *Eublema albifacia* (*Noctuidae*) which get their nourishment through trophallactic exchanges with the workers. Finally, the relationship between *Tetraponera aethiops* (*Pseudomyrmicinae*) and *Barteria fistulosa* (*Passifloraceae*) is presented, demonstrating the protective role of the ant in destroying vines which would otherwise overtake the plant.

LES VIES D'UNE ABEILLE

Roger Darchen

Film 16 mm - Son optique - Durée 26 m.

Ecole d'Apiculture Tropicale - 24260 Le Bugue - France

Lors de son existence une abeille ouvrière occupe des fonctions très variées dans la ruche au point qu'un même individu mène des vies très différentes en peu de temps. Le film a pris ce thème pour fil conducteur général, toutefois la biologie des larves, des mâles et de la reine est aussi largement évoquée.

Film à vocation délibérément pédagogique pour un grand public.

THE LIVES OF A BEE

During her existence, the worker is engaged in various duties in the beehive so much that the same individual leads different lives in a small time.

The film has taken this topic to find the general clues nevertheless the biology of the larvae, the males and the queen has been largely recalled.

The film has been conceived deliberately educational for a large people.

A GUIDE TO THE COLLECTION AND MAINTENANCE OF ANTS.

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Mill Hill, London, NW7 1QS., U.K.

The species *Myrmica rubra*. L. is often used for laboratory experiments, because its Biology is well known and collection and maintenance becomes easier with experience. Students studying ants as well as Naturalists who are just interested in insects, are provided with some background material about ants. Information is also provided about when and where to find *Myrmica*, the equipment necessary for collection, how to collect ants and the types of environment required to keep them in the laboratory or at home. Some experimental investigations which could be carried out in the field as well as in the laboratory are also suggested.

ORCHID POLLINATION BY ORIENTAL HONEYBEE, *APIS CERANA*; A DECEPTION?

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Fascinating attraction scenes of the Japanese honeybee, *Apis cerana japonica* to Oriental orchid, *Cymbidium pumilum*, flowers are introduced in video.

Not only workers but also whole swarming colonies (Sasaki et al., 1993) and drones (Sasaki et al., 1991) are attracted to the orchid. Honeybee drones have long been believed to neither work nor visit flowers. In *A. cerana japonica*, however, drones do visit the orchid flowers and even pollinate it although the chance is significantly lower than that by workers. Attraction of whole swarm is much more spectacular. Racemes (flowers) were completely covered with thousands of bees. Flower petals are wilted by produced heat and sporadic gnawing. However even in such racemes, many flowers are successfully pollinated during "pandemonium" of the visitation.

The orchid has no intrafloral nectary and the bees are attracted and pollinate it without any reward. Bees insert their head and thorax deep into the flowers between column and lip. During their effort to escape from the flower by using middle legs, pollinia stick tightly to the scutellum of the thorax. Thus the phenomenon is thought to be a "deception". Chemical study of the attractive principle is underway and the attractant is not the queen substance. European honeybee, *A. mellifera* is never attracted to the oriental orchid.

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MECHANISMS OF EMANCIPATION OF SLAVES FROM *FORMICA SANGUINEA* COLONIES

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F. sanguinea occasionally makes slaves of wood ants. Just as in the case of typical slave species, mixed colonies originate. Atypical slaves (e.g. *F. polyctena*), however, when their proportion is high enough destroy *F. sanguinea* colonies by eliminating their brood and queens. Then, even though blood-red ant workers are still present, the slaves recruit their own queens. Mechanisms of colony takeover act already when the share of (atypical) slaves is about 50%. The questions are why *F. sanguinea* brood is destroyed and what is the point of queen elimination. Laboratory experiments with mixed colonies of *F. sanguinea* and *F. polyctena* (and their pupae) have shown that the brood is eaten when the ants are short of food (under natural conditions, food shortage appears when the colony size increases rapidly because of mass emergence of callow slaves). *F. sanguinea* pupae are devoured in significantly higher degree than slave pupae. This can be explained by the economics of a mixed society as a whole: the younger brood is eaten first (according to differences in the phenology of the species, *F. sanguinea* pupae are generally younger than *F. polyctena* ones). Mechanism of elimination of blood-red ant queens still remains not clear. Field experiments have revealed that *F. sanguinea* can revive after a few years in colonies of already emancipated slaves. At the same time, in laboratory mixed cultures, *F. polyctena* workers tolerate *F. sanguinea* queens and do not adopt their own ones. The following hypotheses are made: 1) recruitment or rejection of new queens by a mixed society depends not only on the percentage of atypical slaves but on the slave/slaver queen ratio as well; 2) temporary coexistence of probably hostile *F. sanguinea* and wood ant queens may be possible as a form of peculiar bispecific oligogyny (especially in originally monogynous blood-red ant colonies).

EFFECT OF METAL POLLUTION ON THE RED WOOD ANT (FORMICA S. STR.) COLONY DEVELOPMENT

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Considering environmental conservation and biomonitoring, it is important to note that some functional groups of red wood ant workers are loaded with the highest content of metals found among boreal forest animals (Nuorteva, 1990).

Extremely high metal content was recorded in forages in a polluted industrial and mining area of Czechoslovakia (73.4 mg/kg Cd/dwt) (Stary & Kubiznakova, 1987). For comparison, in unpolluted Estonia and Finland regions that was only 7.1 mg/kg. The lowest metal content was determined in reserve ants and females, while negligible amounts were found in the brood (0.1 mg/kg) both in polluted and unpolluted areas. From the phloem of trees metals are also transferred into aphid honeydew that is the most important food for red wood ants. Artificial feeding of ant colonies with metal contaminated honey showed that Cd and Hg inhibit the activity of enzymes participating in ATP synthesis (Migula et al., 1993) on which the formation of energy stores and the development of newly emerged workers into reserve ants is directly based. Therefore, the absence of reserve ants in many nests fed with Cd and Hg contaminated food in 1993 was to be expected. The particularly low level of the metal content in the brood and sexuals gives evidence of the ability of the ant colony to protect their offspring through filtering poisons in the sociobiological self-regulating food chain. Ants possess systems of physiological and sociobiological poison tolerance. This is one of the features offering singular possibilities of survival for social insects, especially in the conditions of a superstructure (polydomous, supercolony).

CHEMICAL COMMUNICATION IN THE JAPANESE HONEYBEE, *Apis cerana japonica* Rad.

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The Japanese honeybee (*Acj*) and the European honeybee *Apis mellifera* L. (*Am*) have been obliged to share the same habitat in Japan since *Am* was introduced in 1877. Scientific studies of *Am* have been conducted worldwide and the resulting literature is extensive. On the other hand, little is known academically regarding *Acj*. In particular, there is little scientific information about *Acj*'s chemical ecology. In this paper, the role played by semiochemicals in *Acj* social behavior was investigated, and the results were compared with *Am*. Social behavior such as alarm behavior, aggregation behavior, and recognition system are controlled by semiochemicals from the sting apparatus, Nasonov gland, feet, and cuticles. Sting apparatus, Nasonov glands, tarsi, and body surfaces were removed from both species. Extracts were analyzed by two different capillary GLCs (CP-Sil 19CB and FFAP) and by GC/MS. Nasonov gland extracts induced aggregation behavior in both species, but GLC profiles of the extracts from *Am* and *Acj* were quite different. A prominent peak in *Acj* extract eluted faster than geraniol, a major volatile component in *Am*. This compound was suggested to be a fatty acid by GC/MS, showing base ion at m/z 60. Similar GLC profiles with isoamyl acetate as the main volatile compound were obtained with sting apparatus extracts, but behavioral responses of worker bees to the extracts were different between the two species. *Am* hydrocarbon profiles were more complicated than *Acj* profiles. However, in both species, even among the same colony's members, hydrocarbon profiles had several different patterns. These results suggest that the differences in compounds and subsequent differences in behavior between *Am* and *Acj* are due to the differences of semiochemicals, sensitivity, and signal processing in the CNS.

WORKER POLICING IN HONEY BEES

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Insect societies are characterized by both conflict and cooperation among nestmates. Conflict and cooperation are consequences of the two non-exclusive means by which workers can enhance their inclusive fitness: 1) **working** to increase the number of reproductives (queens and males) produced by their colony; 2) **manipulating** colony reproduction to favor the production of reproductives of greater kin value. Manipulation is a consequence of the non-clonal kin structure of most insect societies.

In the social Hymenoptera reproductive conflict can occur around diverse aspects of reproduction, of which male production, queen production and sex allocation are probably the most important, and have also received the greatest attention from researchers. In the case of conflict over male production, workers in most advanced eusocial Hymenoptera retain ovaries but cannot mate, and so can only lay male (unfertilized) eggs. Significant production of males by workers in queenright colonies occurs in many (e.g., *Bombus*, *Dolichovespula*, *Melipona*) but not all (e.g., *Apis*, *Vespula*) hymenopteran species. The first prediction from theory is that workers should produce the colony's males, because they are more related to their own sons (0.5) than to the queen's sons (0.25). However, when queens mate with more than two males an individual worker is more related to the queen's sons than to the sons of other workers (<0.25). In this case workers should try to stop each other from reproducing, that is **worker policing** would be favored by natural selection.

Experimental work has shown that worker policing occurs in the honey bee. Workers selectively eat eggs laid by other workers. Egg-recognition is mediated by a queen-produced egg-marking pheromone which marks the eggs laid by the queen, thereby aiding recognition and making removal errors (i.e., removal of queen-laid eggs or non-removal of worker-laid eggs) rare. The pheromone is produced in the queen Dufour gland. Worker policing is likely to occur in other social Hymenoptera (e.g., *Vespula*, *Oecophylla*), but has never been looked for.

Within insect societies, the ability of workers to recognize kin may lead to increased reproductive conflict. (For example, increased ability to recognize full-sisters versus half-sisters would increase the benefits of discriminatory queen rearing in the honey bee and other societies with a single multiply-mated queen.) However, in the context of male production, the ability of workers to recognize queen-laid and worker-laid eggs acts to reduce reproductive conflict. This is because worker policing acts as a counter-manipulation against worker reproduction, thereby reducing the workers' reproductive options to a single option - the rearing of the queen's sons.

In the honey bee worker policing is an effective counter-manipulation because it is not costly. The costs of policing are low for two reasons: (1) errors in egg recognition are low; (2) eggs can be checked easily, because they are contained in open cells. Over evolutionary time the effectiveness of worker policing has led to the comparative rarity of attempted reproduction by honey bee workers. In queenright honey bee colonies of European race only about one worker in 5,000 has well developed ovaries. Nevertheless both worker egg-laying and worker policing go on in normal honey bee colonies, albeit at a rate too low to see unless special observations are made.

Honey bee workers lay large numbers of male eggs in hopelessly queenless colonies, and many of these are reared into adult drones before the colony dies out. In queenless honey bee colonies of European race worker policing breaks down (i.e., worker-laid eggs are accepted) about 3-4 weeks after queen loss. At about the same time, but not before, large numbers of workers have fully developed eggs in their ovaries. Three to four weeks after the loss of the original mother queen is about the time that the colony would become hopelessly queenless by the loss of the replacement sister queen during her mating flights.

INVESTIGATION OF NUCLEIC ACIDS AND POLYPEPTIDES OF CHINESE SACBROOD VIRUS

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Agarose gel eletrophoresis (AGE) and polyacrylamide gel electrophoresis (PAGE) were used to analyze the Chinese Sacbrood Virus (CSBV). The experiment revealed the RNA of CSBV is a single-stranded species which is easily degraded. Its M.W. is 2.8×10^6 daltons. The virus protein consists of three polypeptides with M.W. Of 27,000, 28,000 and 39,000 daltons respectively. The RNA and three polypeptides of the CSBV were different from those of the sacbrood virus from *Apis mellifera* (SBV). Nucleic acid of both CSBV and SBV were performed on the same AGE gel plate simultaneously, and each presented one band. Both R_f showed no difference, when the AGE of CSBV RNA goes on for a certain period of time, the RNA band disappears, but meantime the SBV RNA still shows one band. The SBV protein consists of three polypeptides with M.W. of 24,000, 28,000 and 36,000 daltons respectively.

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L'Union Internationale pour l'Etude des Insectes Sociaux (UIEIS) a été créée voici bientôt un demi-siècle par une poignée de chercheurs européens résolus, en particulier français et allemands. Aujourd'hui, l'Union compte un millier de membres et le congrès de Paris marquera une nouvelle étape de son développement puisqu'elle incorporera nombre de chercheurs de l'ex-Union Soviétique et de la Chine.

Ce développement constant de l'UIEIS traduit non seulement l'intérêt des biologistes pour les sociétés d'insectes mais aussi l'impact de ces derniers sur les écosystèmes naturels ou modifiés par l'Homme.

Le contenu du XII^e Congrès de l'UIEIS, résumé dans cet ouvrage, révèle les tendances les plus marquantes des recherches récentes, vers: l'évolution des comportements sociaux et leurs mécanismes, les relations avec l'environnement, l'histoire naturelle et sa diversité, enfin la biologie moléculaire. D'autres thèmes, jadis développés, ont presque disparu, de nouveaux émergeront demain..

The International Union for the Study of Social Insects (IUSSI) was created almost half a century ago by a handful of determined European researchers, particularly French and German. Today, the Union includes one thousand members and the Congress of Paris will constitute a new step in its development, as it will incorporate researchers from the former Soviet Union and from China.

The constant evolution of IUSSI indicates not only the interest of biologists for insect societies, but the impact of these insects on natural or modified ecosystems.

The content of the XII Congress of IUSSI, summarised in this volume, reveals the main trends of recent research: evolution of social behaviour and analysis of its mechanisms, the relationships between insect societies and their environment, life history and biological diversity, and finally molecular biology. Other themes which were previously well developed have disappeared this time; new ones will emerge tomorrow..

Pierre Jaisson

Président de l'UIEIS / President of IUSSI